A MANUAL OF VETERINARY PHYSIOLOGY

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OF

VETERINARY PHYSIOLOGY

BY

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THIRD EDITION
COMPLETELY REVISED AND IN PARTS RE-WRITTEN

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TO THE MEMORY OF

SIR MICHAEL FOSTER

K.C.B., M.A., M.D., LL.D., D.C.L., F.R.S.

THIS ATTEMPT TO DEAL WITH A BRANCH OF PHYSIOLOGY

IS DEDICATED

IN ACKNOWLEDGMENT OF THE

ENCOURAGEMENT AND ASSISTANCE HE GAVE

THE AUTHOR

IN PROSECUTING THE STUDY OF VETERINARY PHYSIOLOGY

PREFACE TO THE THIRD EDITION

Circumstances beyond my control have delayed the revision of this manual. During the twelve years which have elapsed since the last edition was published considerable additions have been made to our knowledge of physiology. This has necessitated the manual being practically rewritten; only the chapters on the Senses, Locomotion, and the Foot stand nearly as they were; the others have been partly or wholly rewritten.

This book is essentially a veterinary, and not a comparative, physiology. It treats of physiology not only from its theoretical aspect, but from the point of view of clinical utility. The requirements of the student and practitioner have consequently not been lost sight of, and every opportunity has been taken in the text to point out the clinical application of physiological facts. To several chapters a special pathological appendix is added, in order to enforce the lesson that pathology is only physiology out of health. In the chapter on the Nervous System the appendix has been omitted, not because the pathological side is wanting in interest, but for the reason that it is at present so defective in exactitude.

As in previous editions, the horse has been taken as the type. Though he offers so many physiological peculiarities and differences from other animals, still his physiology among quadrupeds must always be of the first importance, and of the greatest practical interest.

By the process of elimination and compression, room has been found for much more material than existed in the previous editions, without adding unduly to the bulk of the book. The digestive system, owing to its extraordinary importance in herbivora, is dealt with very fully.

My cordial thanks are due to Professor Sherrington, F.R.S., who has again very kindly read the Nervous

System, and contributed some new matter on the 'Scratch Reflex' and 'Stepping' in the dog.

My friend Dr. Sheridan Lea, F.R.S., has taken a deep interest in the production of this edition. As an old teacher of physiology he was able to advise me of those points which most students find some difficulty in grasping, and he has rendered the text of these portions clearer and more accurate by his careful revision and additions. He has kindly read all the proofs, amplified the chapter on the Muscular System, and brought the final chemical chapter up to date. I am glad of this opportunity of thanking him for his criticism and invaluable assistance.

Mr. Goodall, F.R.C.V.S., Christchurch, and Mr. Leeney, M.R.C.V.S., Hove, have both been good enough to supply me with information for the chapter on Generation and Development, based on their special experience. For the information contained in the footnote on p. 608 I am indebted to Mr. Leach, F.R.C.V.S., Newmarket.

As a rule no references have been made in the text to published works and papers, excepting where such appeared desirable. The literature of the subject is immense, but I must not omit to mention the help I have obtained from the Manuals and Text-books on Physiology published by Professors Halliburton, Howell (of Baltimore), Starling, Stewart (of Chicago), and from Dr. Leonard Hill's 'Recent Advances in Physiology and Bio-Chemistry.'

The number of figures in the text has been considerably increased, some of them being new and original. I am indebted to Professor Stewart for permission to use many of those illustrating his 'Manual of Physiology,' to Professor Cossar Ewart, F.R.S., for the figures illustrating the early embryos of the horse, and to Messrs. Macmillan for the use of certain figures in Foster's 'Text-book of Physiology' and Huxley's 'Lessons in Elementary Physiology.' My thanks are also due to Messrs. Stahel of Würzburg, for permission to publish Fig. 159 from Dr. Michel's paper 'Zur Kenntnis der Gürber'schen Serum-Albumin-Krystalle.'

F. S.

LONDON, *August*, 1907.

PREFACE TO THE SECOND EDITION

I GREATLY regret the considerable delay which has occurred in the production of this edition, but it has been unavoidable; the work has been rewritten in order to admit of its scope being enlarged, and this has taken longer than I anticipated.

In the revision of the sheets I have received great assistance from Professors M'Kendrick, Halliburton, Haycraft, Sherrington, and Dr. Waller. Professor Sherrington revised the whole of the Nervous System and supplied Figure 58. Professor Mettam, of the Royal Veterinary College, Edinburgh, kindly wrote the chapter dealing with the Development of the Ovum, while to Professor Macqueen, of the London Veterinary College, I am indebted for many useful suggestions and valuable criticism.

To all these gentlemen I offer my cordial thanks; their corrections, suggestions, and criticisms have been of the greatest help, and cannot fail to enhance the value of the book.

As in the first edition, I have avoided dealing with histology, excepting where such was necessary to the clear understanding of the subject under consideration.

After due deliberation, I determined not to introduce for the present the metrical system of weights and measures.

The number of illustrations has been doubled, and for electrotypes of blocks I am indebted to Professor Foster, of Cambridge; Professor M'Kendrick, of Glasgow; Professor Hamilton, of Aberdeen; and Dr. Waller, of London.

The rewriting of this edition has unfortunately necessitated an increase in the size of the book.

WOOLWICH,
September, 1895.

PREFACE TO THE FIRST EDITION

My object throughout this manual has been to condense the information as much as possible, for which purpose I have omitted all special reference to the physiology of the dog, and have not touched upon the histology of the tissues, or methods of physiological inquiry.

The reasons for these omissions are obvious: special canine physiology is of subordinate interest to the profession, and our information about this animal is so complete, that when required no difficulty is experienced in obtaining it from human text-books. The histology of the tissues is already before the profession, and methods of physiological inquiry are only needed for laboratory work, for which purpose this book is not intended.

In the description of the physiology of the various organs and tissues the horse is necessarily taken as the type, but the ox, sheep, and pig are dealt with wherever their special physiology requires it.

It was my original intention to publish nothing until I had gone over the field of equine physiology, but I found after several years of work, that the information I had collected was a mere drop in the ocean, for inquiries of this kind are necessarily slow, and as there appeared no reasonable prospect of covering within the space of one life the ground I had mapped out, I was advised that only good could result from placing on record what little we know of veterinary physiology.

I have, therefore, ventured, I know well how imperfectly, to state the broad facts of the science, so as to render them of use to the student and practitioner. The work does not pretend to be anything more than a stepping-stone to the study of physiology; for those requiring more detailed information, reference must be made to the various text-books of human and comparative physiology which are available.

Incomplete as the work is, it would have been still more so but for the assistance I have received from my friend Dr. Sheridan Lea, F.R.S., of Caius College, Cambridge, who, at great personal inconvenience, has kindly read and revised nearly all the sheets as they passed through the press. In saying this, and expressing to him my very great indebtedness, I in no way wish to shift the responsibility for error or inaccuracy which may exist, but I feel that whatever merit the book possesses is entirely due to him.

I have to thank Professor Michael Foster, F.R.S., for the loan of many of the woodcuts which illustrate this manual, and elsewhere I have acknowledged how much I owe to his encouragement.

To my friend and colleague, Assistant-Professor Butler, A.V.D., my best thanks are due for assistance in revising the proofs, and in the preparation of the index; to Mr. W. Hunting, F.R.C.V.S., for suggestions on the chapter dealing with Locomotion; and to Professor M'Fadyean for the loan of two woodcuts illustrating the chapter on the Foot.

To facilitate the study of locomotion, I have had the plates so arranged as to face as nearly as possible the letterpress describing the movements.

I have laid under contribution Colin's invaluable 'Traité de Physiologie comparée des Animaux'; Ellenberger's 'Physiologie der Haussäugethiere'; Foster's, M'Kendrick's, and Landois and Stirling's Text-books of Physiology; Gamgee's translation of 'Hermann's Physiology'; the same author's 'Physiological Chemistry of the Animal Body'; Halliburton's 'Text-book of Chemical Physiology and Pathology'; Bunge's 'Physiological and Pathological Chemistry'; Meade Smith's 'Physiology of the Domestic Animals,' and others mentioned in the text. With reference to Dr. Meade Smith's work, I regret to find that on page 105 I have inadvertently given the title as 'A Text-book of Comparative Physiology.'

I have endeavoured to acknowledge all sources of information, though it is possible that in drawing from such a wide area I may have omitted in places to do so.

Army Veterinary School, Aldershot,
August, 1892.

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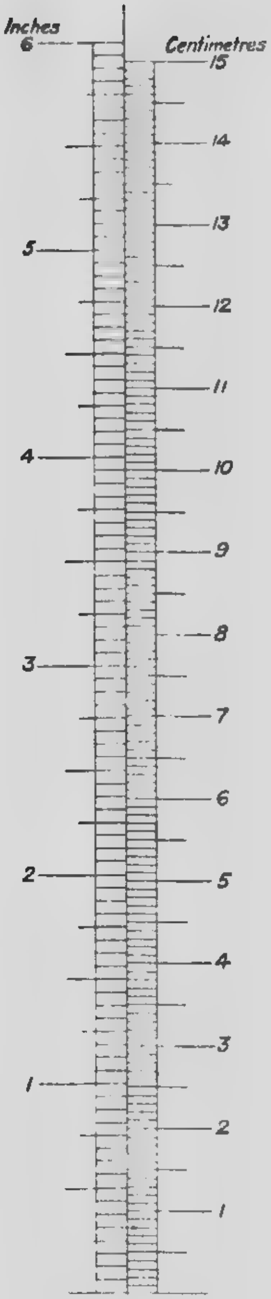
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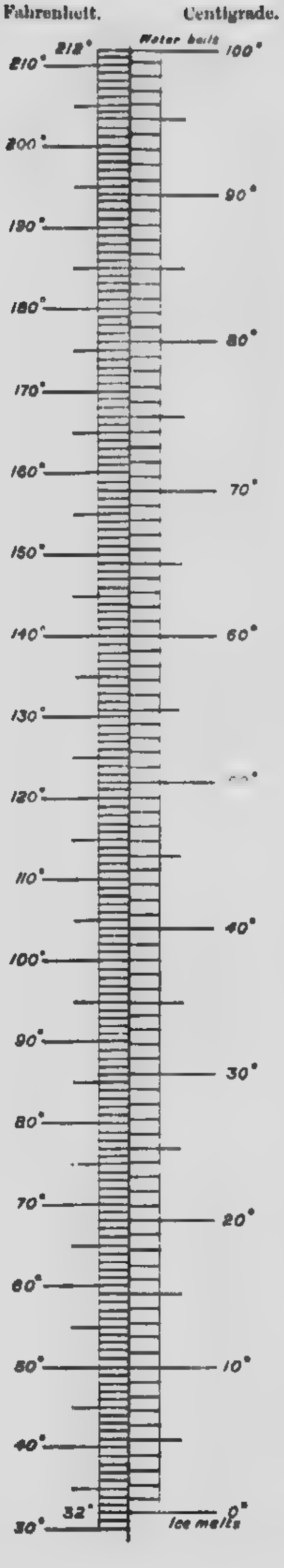
Fahrenheit.
Centigrade.
212°
Water boils
100°
210°
200°
90°
190°
180°
80°
170°
160°
70°
150°
140°
60°
130°
120°
110°
40°
100°
90°
30°
80°
70°
20°
60°
50°
10°
40°
32°
0°
Ice melts
30°

A COMPARISON OF SOME BRITISH AND METRIC UNITS.

Degrees Fahrenheit $= \frac{9}{5}$ C.° + 32.
Degrees Centigrade $= \frac{5}{9}$ (F.° − 32).

Length

1 inch = 25·4 millimetres = 2·54 centimetres.
1 foot = 304·8 ,, = 30·48 ,,
1 yard - - = 91·44 ,,
1 mile = 1609·3 metres = 1·609 kilometres.
5 miles - - = 8 kilometres (nearly).

1 metre = 1,000 millimetres = 39·37 inches.
1 centimetre = $\frac{1}{100}$ metre = 0·39 inch.
1 kilometre = 1,000 metres = 0·62 mile.
8 kilometres - - = 5 miles (nearly).

Weight

1 grain = 0·064 gramme.
1 ounce (avoir.) = 28·35 grammes = 437·5 grains.
1 pound ,, = 453·60 ,, = ½ kilogramme (approx.).
1 cwt. ,, - - - = 50·8 kilogrammes.
1 ton ,, - - - = 1,016 ,,

1 kilogramme = 1,000 grammes = 2·2 pounds (avoir.).
1 gramme - - - = 15·432 grains.
1 milligramme = $\frac{1}{1000}$ gramme = 0·0154 grain.

Capacity

1 fluid ounce = 28·4 cubic centimetres.
1 pint = 568·0 ,, ,,
1 gallon = 4·54 litres.
1 peck = 9·08 ,,
1 bushel = 36·32 ,,
1 cubic inch = 16·38 cubic centimetres.
1 ,, foot = 28·31 litres.

1 litre = 1,000 cubic centimetres = cubic decimetre = 1·76 pint (imperial).
1 cubic centimetre = 0·061 cubic inch.
1 cubic metre = 1,000 cubic decimetres = 35·3 cubic feet.

Work

1 foot-pound = 0·138 kilogramme-metre.
1 foot-ton = 309·12 ,, ,,

1 kilogramme-metre = 7·23 foot-pounds.

1 unit of heat (British) = heat necessary to raise 1 pound of water through 1° F.
1 calorie (Metric) = heat necessary to raise 1 gramme of water through 1° C.
Mechanical equivalent of heat-unit = 772 foot-pounds.
,, ,, calorie = 424 gramme-metres.
,, ,, kilo-calorie = 424 kilogramme-metres.

CORRIGENDA

Page 19, top line, *for* 'action' *read* 'difference.'
,, 59, line 7 from bottom, *for* 'all' *read* 'during.'
,, 94, line 17 from bottom, *for* 'occupy' *read* 'occupying.'
,, 140, line 19 from top, *for* 'Appendix' *read* 'Chapter XX.'
,, 171, footnote, 'H. J. Brown' *should be* 'H. T. Brown.'
,, 185, line 10 from bottom, the semicolon *to be* a comma.
,, 225, line 9 from top, *after* 'such' *insert* 'power.'
,, 337, bottom line, *for* 'come' *read* 'comes.'
,, 429, line 5 from bottom, *for* 'dilatation' *read* 'dilating.'
,, 439, line 2 from bottom, *for* 'cochlea' *read* 'cochlear.'
,, 472, line 8 from bottom, *for* 'revolves' *read* 'rotates.'
,, 584, line 18 from top, *for* 'kreatine' *read* 'creatine.'
,, 636, line 15 from top, delete comma *after* 'albumin.'
,, 636, line 22 from top, delete hyphen *after* 'blood.'
,, 637, line 10 from top, *for* 'albumose' *read* 'albumoses.'
,, 637, line 14 from top, *for* 'alchol' *read* 'alcohol.'

A MANUAL OF VETERINARY PHYSIOLOGY

CHAPTER I

THE BLOOD

The special functions of the blood are to nourish all the tissues of the body, and thus aid in their growth and repair; to furnish material for the purpose of the body secretions, to supply the organism with oxygen, without which life is impossible, and finally to convey from the tissues the products of their activity. To enable all this to be carried out the blood is constantly in circulation, is rapidly renewed, is instantaneously purified in the lungs and, by means of certain channels, is placed directly in communication with the nourishing fluid absorbed from the intestines, by which it is constantly repaired.

Physical Characters.—Blood is a red, opaque, rather viscous fluid, the tint of which depends upon whether it is drawn from an artery or a vein; in the former it is of a bright scarlet colour, whilst in the latter it is of a purplish red. The colour is due to a pigment called hæmoglobin contained in the red corpuscles. Whether the colour is scarlet, as in blood from an artery, or purplish, as from a vein, depends on the difference in the amount of oxygen with which the hæmoglobin is combined.

The reaction of blood is alkaline; as the process of coagulation occurs this alkalinity diminishes. The alkaline reaction is due to the phosphate and bicarbonate of soda found in the fluid; the decreasing alkalinity observed on standing is probably due to the formation of an acid. The alkalinity of the blood is reduced by muscular work, owing to the production of an acid by the muscles.

The odour of blood is believed to be due to a volatile body of the fatty acid series. The blood of the cat and dog has a peculiar and decidedly disagreeable smell; this is not observed in the blood of the horse and ox, though it is said that the odour of butyric acid can always be obtained from the blood of the latter by heating it with sulphuric acid. The taste of blood is saltish, due to the amount of sodium chloride it contains.

The specific gravity varies in different animals: in the horse, ox, and pig, 1060; sheep, 1050-1058; dog, 1050 (Colin). According to Hoppe-Seyler the specific gravity of the liquor sanguinis of the horse is 1027 to 1028, and the specific gravity of the cells 1105. This considerable difference between the specific gravity of the cells and the liquor sanguinis in the horse, accounts for the rapid manner in which the cells sink in horses' blood when drawn from the body, producing during the process of clotting the so-called 'buffy coat.'

The **composition of the blood** is almost absolutely uniform so far as the presence of various substances is concerned; the amount of these substances, however, varies in animals of different classes. The source from which the blood is taken also affects its composition; the blood from an artery does not represent exactly that found in a vein.

Blood consists of:

1. A fluid part, Liquor sanguinis or Plasma, containing in solution proteids, extractives, mineral matter and gases, the latter in a state of loose chemical combination.
2. Corpuscles.
    - α. Red corpuscles.
    - β. White corpuscles.
    - γ. Platelets.

The **Liquor Sanguinis**, or **Plasma**, forms about 66 per cent. of the total blood; it is an albuminous fluid containing a small and variable amount of a yellow colouring matter of a fatty nature. It holds in solution three proteids—viz., fibrinogen, serum globulin (paraglobulin), and serum albumin. Recent researches have shown that what has always been regarded as serum globulin consists in reality of two proteids, to which distinctive names have been given.

It is a simple matter to separate these proteids from plasma, as they are differently acted upon by neutral salts. For example, fibrinogen is precipitated by half saturation with common salt, serum globulin is precipitated by saturation with magnesium sulphate, serum albumin may be wholly precipitated by ammonium sulphate.

During the life of the blood the liquor sanguinis is termed the plasma, but after it has been shed from the body and coagulation has occurred, the liquid residue is called serum. **Serum** is, therefore, plasma which is modified as the result of coagulation, and as this latter process is attended by the production of fibrin, we may say that serum is plasma minus the fibrin-forming elements. Perhaps the nearest approach to pure plasma is the fluid found in the pericardium and abdominal cavity.

The fluid effused into the pleural cavity during pleurisy is plasma to start with, but if the fibrin in it becomes thrown down (forming the so-called false membranes), the remaining fluid is serum which is no longer capable of clotting.

The **Proteids of Serum** are serum globulin, serum albumin, and a ferment produced as the result of coagulation. As fibrinogen is used up in the process of coagulation it is not found in serum, but a proteid known as fibrino-globulin appears, though in small quantities. Fibrino-globulin is produced from fibrinogen during the process of fibrin formation. In the following table a comparison is made between the proteids of the plasma and serum:

Proteids of the Plasma.	*Proteids of the Serum.*
Fibrinogen.	Serum globulin.
Serum globulin.	Serum albumin.
Serum albumin.	Fibrin ferment (nucleo-proteid).
	Fibrino-globulin.

It has been shown that the proportion in which serum globulin and serum albumin exist in the blood varies in different animals. In the horse and ox the globulins are in excess of the albumins; in man and the rabbit this is reversed. Analyses show that the amount of total proteids is rather more uniform than is that of the different albumins of which they are composed, as may be seen from the following table, which represents the weight of proteid (grammes in 100 c.c.) of blood plasma of different animals:

	Total Proteids.	*Serum Albumin.*	*Para-globulin.*	*Fibrinogen.*
Dog - - -	6·03	3·17	2·26	0·60
Sheep - - -	7·29	3·85	3·00	0·46
Horse - - -	8·04	2·80	4·79	0·45
Pig - - -	8·05	4·42	2·98	0·65

Fibrinogen is the precursor of fibrin, a substance of which we shall have more to say when dealing with coagulation; it is found in blood plasma, but not in the serum, since it is converted into fibrin during the process of clotting; it also exists in the fluids exuded into the cavity of the chest, pericardium, etc.

Corpuscles.—Blood examined under the microscope is found to consist of an enormous number of bodies termed corpuscles floating in the liquor sanguinis. These corpuscles are of two kinds, red and white; the former are the more numerous, the latter are the larger.

The **Red Corpuscles** constitute 33 per cent. or one-third of the total blood. Viewed under the microscope, they are found to be biconcave discs, circular in shape, and possessing no nucleus (Plate I.); they are soft, flexible, elastic bodies, capable of having their shape readily altered by pressure, which enables them to pass along the finest capillaries. The colour of a single corpuscle is yellow, but when heaped together they are red, and thus give the colour to the blood.

In all mammals excepting the Camel tribe the red cells are circular; in all vertebrates below mammals they are biconvex, oval, and nucleated. The corpuscles vary in size in different animals, as may be seen in the diagram (Fig. 1). When a drop of blood is shed, the red cells at first move quite freely each over the other. In a short time they tend apparently to become sticky, and when this state is reached they have a tendency to lie in long rows, with their flat surfaces in close contact, resembling the appearance of a pile of pennies. This condition is not marked in horses' blood.

A red blood-cell is composed of a spongy stroma, holding in its meshes the red colouring matter. The stroma or framework of the corpuscle consists chiefly of nucleo-albumin, and also contains lecithin, cholesterin, and salts; the red colouring matter consists of an albuminous crystalline substance, hæmoglobin, which forms no less than 90 to 94 per cent. of the total solid matter of the dried corpuscle.

Fig. 1.—Diagram showing Relative Size of Red Corpuscles of Various Animals (Stewart).

The number of corpuscles in the blood is determined approximately either by the method of Gowers or Malassez. The principle on which these methods are based is the same—a known quantity of blood is diluted with a known bulk of artificial serum and thoroughly mixed; of this a small drop is placed in a counting-chamber, which is ruled into squares, and examined under the microscope. The blood cells occupying the squares are counted, as may readily be done, and the mean of them taken. In the horse the mean number of red blood corpuscles per cubic millimetre is 7,212,500, and in the ox 5,073,000. Taking the amount of blood in the horse as 66 lbs. (50 pints or 29 litres), this gives 204,113,750,000,000 as the approximate number of red cells in the body (Ellenberger).* It is evident that a loss of water from the blood means a larger relative proportion of red cells present, while an excess of water by diluting the blood would show a loss of red cells; thus the number of the red cells is increased by sweating, by the excretion of water from the bowels and kidneys, and by starvation, while it is diminished by pregnancy and copious draughts of water. But apart from these conditions, it is undoubted that an actual increase or decrease in the number of red cells may occur, this numerical variation being especially marked in some diseases. The shape of the red cell is affected by the amount of fluid in the plasma—if the latter be artificially concentrated water diffuses from the corpuscle to the plasma, and in consequence it shrinks and becomes wrinkled. If the plasma be diluted the red cells swell. A ·9 per cent. solution of sodium chloride causes the corpuscles neither to shrink nor swell; this strength is known as 'physiological salt solution,' and may be employed for the purpose of transfusion.

Each red cell offers a certain absorbing surface for oxygen, which, if calculated on the total number of corpuscles, is something enormous, being equal for the horse to a square having a side of 180 yards. The opacity of blood is due to the red cells reflecting light as the result of their peculiar shape; if the cells be destroyed either by freezing and thawing the blood alternately, or by the passage through it of electric shocks, or by the addition of certain agents such as chloroform, ether, bile salts, water, tannic or boric acids, etc., the hæmoglobin becomes liberated from the broken-up cell and stains the naturally yellow plasma of a red colour. Further, the destruction of the corpuscles leads to the blood becoming transparent or, as it is termed, 'laky.'

The greater part of the red cell consists, as already stated, of hæmoglobin, a substance possessing a remarkable affinity for oxygen: this it obtains at the lungs and leaves behind it in the tissues. The hæmoglobin of the red cells, therefore, exists in two states, one in which it is charged with oxygen called oxy-hæmoglobin, and the other in which it has lost its oxygen and is known as reduced hæmoglobin. The process of oxidation in the lungs and reduction in the tissues is constantly occurring at every cycle of the circulation, with the ultimate result that the red blood disc gets worn out and dies. In this condition it is cast off from the system, being got rid of through the medium of the liver, and also, probably, destroyed in the spleen and elsewhere. When the red cells die their hæmoglobin is set free, and decomposed into an iron-free residue from which, probably, all the pigments of the body are formed, especially those of the bile.

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* 'Physiologie der Haussaugethiere.'

The production of red cells is a matter of extreme rapidity, as may be witnessed, for example, after hæmorrhage; the seat of their formation is in the red marrow of bones, where they are formed from certain nucleated cells; there are several varieties of cells in the red marrow, and it is not quite definitely settled which of these furnish the red blood cells. All other seats of formation are doubtful, though it should be mentioned that the formation of red cells from blood platelets in the blood stream has been put forward as of possible occurrence. In the embryo the future red cells for a certain period are nucleated and contain no hæmoglobin, but these are gradually replaced by non-nucleated hæmoglobin-holding corpuscles before birth. It is interesting to observe that both in the embryo and in the adult the red cells are derived from a nucleated precursor.

Blood Platelets are small bodies one-quarter the size of a red cell, which have been observed in the circulating blood, but can also be seen immediately after the blood is shed. They have been supposed by some to be the precursors of the red cells, but this point is not as yet settled.

We have mentioned that the red colouring substance hæmoglobin is retained in the pores of the stroma of the red cells, and with this we must now deal.

Hæmoglobin is a most remarkable substance. It is a proteid, distinguished from the majority of the other members of its class by the comparative ease with which it may be obtained in a crystalline form, whilst, on the other hand, its behaviour in a dialyser is not that of a crystalloid but of a colloid. It is one of the most complex substances in organic chemistry, containing C, H, O, N, S, and Fe, and its molecule is an enormous one, the molecular weight being quoted at 13,000 to 14,000. Crystals of hæmoglobin when seen in bulk are of a dark-red or bluish-red colour; they are extremely soluble in water, the solution being dichroic—viz., green by reflected and bluish-red by transmitted light. Hæmoglobin is remarkable as being the most important proximate constituent of the body containing iron, the amount being about ·4 per cent. The source of the iron is not settled, but there is an organic iron-containing substance in food known as *hæmatogen*, belonging to the nucleo-albumin group, which possibly furnishes it. Its formation from inorganic iron is probably of doubtful occurrence.

The total amount of hæmoglobin in a horse's body is about 8·8 lbs. (4 kilogrammes), and the amount of iron contained in this is about 257 grains (17 grammes). This calculation is based on the assumption that the amount of blood in the body is 66 lbs.

In the dried red blood cells hæmoglobin exists in the proportion of 90 to 94 per cent., in the corpuscle under normal conditions it represents 32 per cent. of its weight, while in the total blood of the horse it forms 13·15 per cent., in the ox 9·96 per cent., sheep 10·34 per cent., pig 12·7 per cent., and dog 9·77 per cent. (Ellenberger).* The younger the animal the less hæmoglobin; males have more than females, and castrated animals more than entires (G. Müller).†

Hæmoglobin has a remarkable affinity for oxygen, and the ordinary laws relating to the absorption of gases by fluids and solids do not apply—as we shall see later when dealing with Respiration—to the absorption of oxygen by hæmoglobin. According to Bohr, hæmoglobin can absorb carbon dioxide, which combines with the globulin portion of the molecule.

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* 'Physiologie der Haussäugethiere.'

† *Ibid.*

We have mentioned that when hæmoglobin is charged with oxygen it is spoken of as oxy-hæmoglobin; when it has discharged its oxygen, which it is capable of doing with considerable facility, it is described as reduced hæmoglobin, or simply as hæmoglobin. As oxy-hæmoglobin it is charged with oxygen in the capillaries of the lungs, brought back to the heart and distributed all over the body; in the tissues it gives up its oxygen, and as partially reduced hæmoglobin is brought back by the veins to the heart for distribution to the lungs, where it renews its oxidized condition. Hæmoglobin is never completely reduced in the body excepting in the last stage of asphyxia.

Oxy-hæmoglobin crystallises in some animals, horse, cat, dog, and guinea-pig, with facility; in others, ox, sheep, and pig, with difficulty. The crystals are generally rhombic plates and prisms, but the form differs according to the animal (Fig. 2). Reduced hæmoglobin can only be crystallised with great difficulty in an atmosphere free from oxygen.

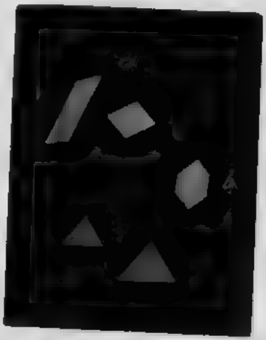

FIG. 2.—CRYSTALS OF HÆMOGLOBIN —*a*, HUMAN; *b*, SQUIRREL; *c*, GUINEA-PIG (STEWART).

When examined by the spectroscope the two hæmoglobins produce quite distinctive spectra, by which they may be readily recognised. To put the matter broadly, oxy-hæmoglobin gives two well-marked dark absorption bands or shadows in the green portion of the spectrum, one band being wide, the other narrow; while reduced hæmoglobin gives one wide single band in nearly the same position (Fig. 3). Oxy-hæmoglobin may readily be reduced to hæmoglobin by the addition of Stokes's Fluid (an alkaline solution of ferrous tartrate).

Oxygen and hæmoglobin are so lightly bound together that they are readily separated; oxygen is given off if the blood be placed in a vacuum or boiled, or if it be brought into contact with indifferent gases such as nitrogen and hydrogen; it is the facility with which hæmoglobin parts with its oxygen which enables the tissues to obtain it.

Hæmoglobin forms certain compounds with oxygen, carbon monoxide, and nitric oxide:

With oxygen it forms oxy-hæmoglobin and methæmoglobin.
„ carbon monoxide it forms CO hæmoglobin.
„ nitric oxide „ NO „

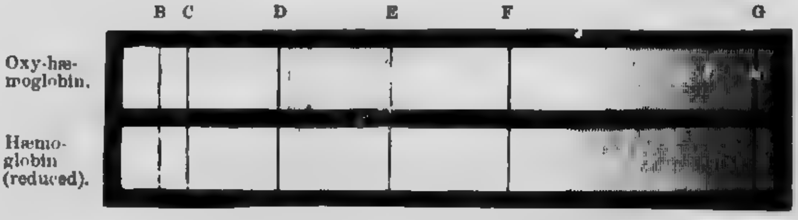

FIG. 8.—BLOOD SPECTRA (WALLER).

Oxy-hæmoglobin we have dealt with; the others, in a work of this kind, can only receive a short notice at our hands, though the subject is full of interest.

Methæmoglobin is produced by allowing blood to be exposed to the air until it becomes brown in colour and acid in reaction; or it may be prepared by the action of acids or alkalies on oxy-hæmoglobin. This substance separates from its oxygen with difficulty, and gives a three-banded spectrum. Methæmoglobin does not occur normally in the body, but may be found in the urine whenever a sudden breaking down of red corpuscles occurs, as, for example, in the so-called azoturia of the horse.

Carboxy-hæmoglobin.—In this compound the oxygen is replaced by carbon monoxide, which forms a stable compound with the hæmoglobin and is not displaced on breathing oxygen; hence the rapidly fatal results of this form of poisoning. The blood of people who have died from CO poisoning is of a cherry-red colour, and yields the spectrum of CO-hæmoglobin—viz., two bands very much like those of oxy-hæmoglobin, though somewhat darker and situated slightly nearer to the violet end of the spectrum. These two bands are unaltered by Stokes's Fluid. **Nitric oxide hæmoglobin** in many respects resembles CO-hæmoglobin.

Hæmoglobin is easily decomposed either by boiling or the addition of alkalies, acids, or acid salts; in either case it splits up into a substance containing the iron, known as **hæmatin**, and a proteid substance or substances termed **globin.** Hæmatin in the dry state strongly resembles iodine in appearance; it has a metallic lustre, a blue-black colour, is not crystallisable, and yields, when pulverised, a dark brown powder which contains 8·82 per cent. of iron. Hæmatin is a remarkably stable substance, and the colouring matter presents a distinctive spectrum both in an acid and alkaline solution. Alkaline solutions of hæmatin can take up and give off oxygen like hæmoglobin. When hæmatin is treated with glacial acetic acid and common salt it yields **hæmin**, which, when examined microscopically, is found to consist of prismatic crystals, dark, or nearly black in colour. Hæmin crystals may be readily produced by warming the dried blood with a drop of glacial acetic acid on a slide; this is used as a microscopical test, but it is said that from the blood of the ox and pig hæmin can only be obtained in very irregular crystalline masses.

When reduced hæmoglobin is decomposed by acids or alkalies, oxygen being carefully excluded, it yields **hæmochromogen**, a substance presenting a definite spectrum and thus a ready means of detecting old blood-stains. **Hæmatoporphyrin** is obtained by the action of strong sulphuric acid on hæmatin, which thereby loses its iron; hæmatoporphyrin is really hæmatin from which the iron has been removed; it is isomeric with bilirubin.

Hydrobilirubin is obtained by the action of reducing agents on hæmatin; it very closely resembles urobilin, a pigment found in urine.

Hæmatoidin (Fig. 4) is found in old blood-clots and in the ovary; it is a crystalline iron-free product derived from hæmatin, and gives the same reaction with nitrous acid as bile pigment, viz., a play of colours. Hæmatoidin is, in fact, chemically identical with bilirubin, and the name is now of interest merely as indicating the close genetic relationship of the pigments of bile to the colouring matter of blood. Notwithstanding this close relationship, it has not as yet been found possible to convert hæmatin into bilirubin. The nearest approach to bilirubin is iron-free hæmatin (hæmatoporphyrin). Again, both hæmatin and bilirubin may be made to yield an identical product (hydro-bilirubin); this product closely resembles urobilin, a pigment found in the urine, and urobilin beyond all doubt is derived from bilirubin in the digestive canal, under the influence of putrefactive organisms.

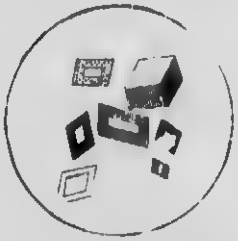

FIG. 4.—CRYSTALS OF HÆMATOIDIN (STEWART).

The **White Corpuscles**, also termed leucocytes, are found in blood, lymph, pus, connective tissue, etc.; they exist in blood in the proportion of 1 in 300 to 1 in 700, the proportion varying according to the vessel from which the blood is examined. In the splenic artery there are very few, in the splenic vein they are exceedingly numerous. Blood which has been removed from the vessels contains but few, for the reason that they are probably broken down during the formation of fibrin.

The white corpuscle is somewhat larger than the red; it consists of a granular-looking protoplasm, within which is a nucleus; the nucleus shows no sign of a nuclear network, which is a distinguishing difference between the white cell and its very close ally the lymph cell. The granular condition of the corpuscle is due to minute particles of fat, proteid, and probably other substances, which are on their way either to or from the tissues, probably both. There are at least five varieties of colourless corpuscles: (1) The *polynuclear*, which are very numerous and consist of a cell containing two or three nuclei united by fine threads; (2) *hyaline leucocytes*, relatively few in number, containing a single nucleus and more protoplasm; (3) *eosinophile* cells, consisting of large masses of granular protoplasm with a simple or lobed nucleus: the granules stain deeply with eosin; (4) *lymphocytes* derived from the lymphatic glands containing a large spherical nucleus and limited protoplasm; (5) *basophile leucocytes*, which are very rare and distinguished by staining with basic dyes and a methylene blue (Plate I.).

The white corpuscles are capable of undergoing changes in shape; the movements known as *amœboid* are exhibited by projections shooting out from the surface and being again retracted (Fig. 5). The amœboid movements are destroyed by heat or by shocks from an induction coil. These changes in shape assist materially in the passage of the corpuscles through the walls of the vessels into the tissues. The process is termed *diapedesis;* within moderation it is a perfectly normal phenomenon, though under inflammatory and other disturbing influences it becomes greatly exaggerated. The white corpuscle has the power of taking up into its interior small particles of colouring matter, bacteria, etc., the importance of which will presently be alluded to.

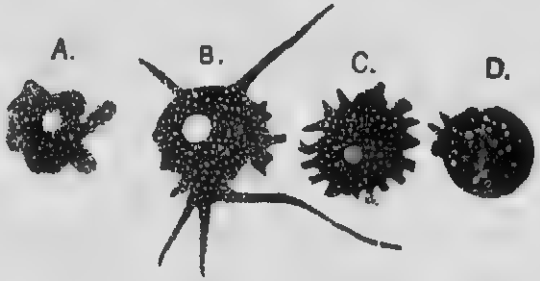

FIG. 5.—AMŒBOID MOVEMENT.
A, B, C, D, Successive changes in the form of an amœba (Stewart).

The white corpuscles contain about 10 per cent. of solids. The cell protoplasm consists of proteids belonging to the globulin and nucleo-proteid groups, while the nucleus consists of nuclein which is remarkable as being a very stable substance and also as containing phosphorus. The nucleo-proteid obtained from the protoplasm is probably the precursor of the fibrin ferment. Besides these we have the complex fatty body lecithin, cholesterin, glycogen (especially in the horse), salts of potash and phosphates, the latter being probably derived from the phosphorus-containing compounds.

The origin of the white corpuscles is from the lymphatic system, from which they enter the blood stream through the large lymphatic channels opening into the vena cava at the junction of the two jugular veins. The hyaline corpuscles are derived from the lymphocytes, the polynuclear and eosinophile produce themselves in the blood stream by cell division. The white corpuscles, as well as the red, are constantly being used up and as constantly replaced. They also possess the power of passing through the walls of the vessels into the surrounding tissues, from which they are removed by the lymph channels, and so find their way back to the blood. No doubt many corpuscles leave the blood the destruction of which we are unable to account for, but it is suggested that by their death they influence the composition of the blood plasma, as in this fluid their component parts must become dissolved after their death.

During the life of the white corpuscle great activity prevails; it is constantly giving up and taking in material which must affect the composition of the plasma. It is known that the white cell possesses the power of digesting certain substances, both solid and liquid. The researches of Metschnikoff have paved the way towards a better understanding of the probable manner in which protection against certain diseases is obtained. He has shown that the white cells take up the bacteria into their interior and digest them; it is really a fight between bacteria and leucocytes. The protection afforded to the system by the white blood cells is, therefore, not the least important of the functions performed by them, and whether they accomplish this duty thoroughly or imperfectly depends largely on the composition of the blood plasma (see p. 26).

Coagulation.—We are now brought to a consideration of the subject of blood-clotting, a process by which the naturally fluid blood becomes converted into a solid.

If blood be drawn from the body and left at rest, it will be found within a few minutes to have undergone the process of clotting. The fluid first becomes a jelly and then a firm clot or crassamentum, taking a complete cast of the vessel in which it is placed, and so firm in consistence that it may be inverted without any blood being lost. In a short time the clot begins to contract, and by so doing squeezes out a fluid known as serum (Fig. 6). This gradually accumulates, and as it becomes abundant the clot sinks. The blood of the horse is remarkable for the slow rate at which coagulation occurs, and the red cells, being specifically heavier than the plasma, have time to fall in the fluid before the process is completed. The result of this is that the upper solid layer is considerably decolourised, forming the so-called **buffy coat**, which though natural to the blood of the horse, is indicative in other animals of the presence of an inflammatory process in the system.

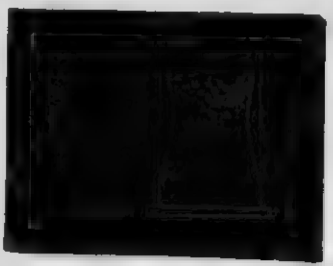

FIG. 6.—DIAGRAM OF CLOT WITH BUFFY COAT (STEWART).

r, Lower portion of clot with red corpuscles; *w*, white corpuscles in upper layer of clot; *c*, cupped upper surface of clot; *s*, serum.

We have here closely followed the account given by human physiologists of the coagulation of the blood in the horse, but the appearance described is by no means invariable. Coagulation in this animal is often complete in less than five minutes, when, of course, no buffy coat forms, and we are inclined to believe that rapid coagulation and non-buffy coat are the rule rather than the exception; we have repeatedly observed the blood of the horse clot so rapidly as to be almost instantaneous. One thing in connection with horse's blood is undoubted, and that is that coagulation is more easily slowed or prevented by cold and neutral salts than it is in the blood of any other warm-blooded animal. May it not be that some confusion has thus arisen, and we have come to regard this abnormally easy slowing of clotting by cold and salts, as if it were markedly a characteristic of horse's blood as it clots naturally?

According to Nasse, the average time occupied in coagulation is as follows:

Pig - - -	¼ to 1½ minutes.
Sheep - - -	½ ,, 1½ ,,
Dog - - -	1 ,, 8 ,,
Ox - - - -	5 ,, 18 ,,
Horse - - -	5 ,, 18 ,,

In our experience the extreme time mentioned for the horse is exceptionally long.

If the clot be examined microscopically it is found to consist of fine fibrils, entangled in which are the blood corpuscles; if the fibrin produced be washed completely free from blood, its appearance is well described by its name.

If instead of allowing the blood to clot spontaneously it be whipped with a rod or bunch of twigs, or, as we say, is 'defibrinated,' the fibrin separates rapidly and coats the rod, while no coagulation in the remaining fluid can occur. The power of spontaneous clotting lies, then, in the production of fibrin.

These changes may be graphically represented thus:

On Clotting.

- Blood.
  - Plasma.
    - Serum.
    - Fibrin. } Clot.
  - Corpuscles.
    - Red. } Clot.
    - White. } Clot.
    - Blood platelets. } Clot.

When Whipped.

- Blood.
  - Plasma.
    - Fibrin.
    - Serum. } Defibrinated blood
  - Corpuscles.
    - Red. } Defibrinated blood
    - White. } Defibrinated blood
    - Blood platelets. } Defibrinated blood

Fibrin is a yellowish-white, stringy-looking, bulky mass. It may be dissolved by dilute hydrochloric acid, forming acid-albumin or syntonin, also by dilute alkalies with the production of alkali-albumin, and by the prolonged action of neutral salts, with the formation of globulins. Its bulky appearance would lead to the belief that it exists in blood in large quantities; it is found, however, to be by weight relatively small. In human blood its proportion is ·2 per cent.; sheep, ·2 to ·3 per cent.; ox, ·3 to ·4 per cent.; horse, ·4 per cent.; pig, ·4 to ·5 per cent.; dog ·2 per cent.

The Cause of Coagulation has kept physiologists busy for many years, and even at the present time the matter has by no means been settled. The theory most generally accepted is that of Hammarsten—viz., that clotting is due to the conversion of a fluid fibrinogen into a solid fibrin, under the influence of a ferment.

If blood be prevented from coagulating plasma can be obtained, and this plasma, depending upon the agents used in its production, will teach us the main facts of coagulation. If it be obtained by cooling the blood, then the plasma will clot spontaneously by allowing the temperature to rise; if the plasma be obtained by previously mixing the blood with a definite amount of magnesium or sodium sulphate, or common salt, clotting can be obtained by diluting it. If it be obtained by acting on blood with oxalates, then clotting can be brought about on the addition of a lime salt, and if it be peptone plasma (see p. 20), simple dilution will cause it to clot. The clot formed by the plasma coagulating is precisely the same as that formed by the blood coagulating; it is of course colourless.

If the above plasmas be acted upon by adding common salt to saturation, a precipitate of fibrinogen occurs; it is a proteid belonging to the globulin group, and has previously been alluded to. If this precipitate be re-dissolved by diluting the fluid and allowed to stand, it clots spontaneously. If a solution of pure fibrinogen be prepared, it does not clot spontaneously, but it may be made to do so by the addition of a drop of serum or the washings of a blood-clot.

The interpretation of all this is that the substance which brings about coagulation of the blood is contained in the plasma. This substance is fibrinogen, but fibrinogen will not work alone; it requires a very small quantity of something else, and this something has been termed the **fibrin ferment.** It is called a ferment inasmuch as a very small amount of it is capable of acting on an indefinitely large amount of fibrinogen, and that its action is closely dependent on temperature.

The ferment is known as **thrombin**; it does not exist as such in the living blood, but can readily be obtained from blood which is shed. Thrombin can be injected into the general circulation without producing any ill effect. Experimental inquiry shows that there is in the blood a precursor of thrombin spoken of as **pro-thrombin,** and that under the influence of calcium salts the pro-thrombin is converted into thrombin. In fact, under the influence of calcium salts, any of the tissues of the body, especially lymphatic glands, will provide a thrombin. The substance from which this thrombin is obtained is known as nucleo-albumin, and if nucleo-albumin be injected into the blood-stream clotting at once occurs.

Chemically very little is known of the blood ferment beyond the fact that heating to 131° F. (55° C.) destroys it. The substance from which it is formed, pro-thrombin, is rich in phosphorus and contains nuclein. Histologically pro-thrombin appears to be identical with blood platelets, and the latter may be observed, when repairing the damaged wall of a bloodvessel, to plug it with a substance resembling fibrin in appearance. It is, in fact, by this means that hæmorrhage gradually tends to cease.

Circumstances influencing Coagulation.—It is a matter of common observation, that after death the coagulation of blood in the vessels is a slow process, though by exposure to air clotting is almost at once produced. At one time it was supposed that the air in some way influenced this, but it has been shown that the action is due rather to the influence on the blood exerted by the wall of the vessels. The jugular vein of a horse may be included between ligatures and excised (Fig. 7), yet the blood will remain fluid in it for one or two days, though suspended in such a way as to be left freely exposed to the air; nevertheless on removal from the vein clotting at once occurs.

When bloodvessels are injured during life, or when pathological changes occur in the blood, coagulation inside the vessels will take place: this is due to the influence exercised over the blood by the injured vascular wall which acts as a foreign body.

Clotting in shed blood may be retarded or hastened by certain conditions. The blood of a horse received into a vessel so constructed as to expose it to a freezing temperature may be kept fluid for an indefinite period, though coagulation will at once occur when the temperature is allowed to rise. Clotting is delayed by the addition to the blood of the neutral salts of the alkalies and alkaline earths, and of ammonium. The addition of dilute acetic acid or the passage of a current of carbonic acid entirely prevents it, by precipitating the fibrinogen. On adding to blood even a weak solution of potassium oxalate, calcium oxalate is formed and clotting prevented, as without the calcium salt no fibrin can be produced. It has been shown that the administration of citric acid to the living animal renders the blood uncoagulable, and this it effects by binding up the lime salts. Conversely, the addition of lime salts to the blood increases the coagulability of the fluid.

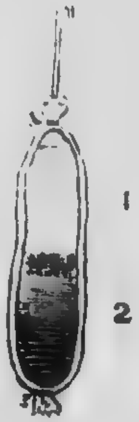

Fig. 7.—Jugular Vein of the Horse ligatured and removed from the Body, known as the 'Living Test-Tube' Experiment.

1, Plasma; 2, red corpuscles which have settled, and in the upper layer of which the white corpuscles are entangled.

In the curdling of milk by the addition of rennet, the presence of a calcium salt is also absolutely essential. The similarity between milk curdling and blood clotting has been recognised for many years. If peptone be injected into the blood of the dog such blood will not clot, and much the same effect is produced if, instead of peptone, an extract of the ordinary medicinal leech be used. The peptone blood refuses to clot not on account of the peptone as such, but for the reason that the peptone causes a secretion from the liver of a substance which prevents coagulation. The leech extract acts by destroying the ferment.

By rapidly heating blood to 133° F. (56° C.), the fibrin-forming substances are precipitated, and clotting is prevented. It is also considerably retarded if the blood as it is shed from the living animal is collected in a vessel the walls of which are thinly coated with oil. The layer of oil apparently acts as an 'inert' substance towards the blood, thus resembling the inner wall of an uninjured bloodvessel. The shape of the collecting vessel has an influence over coagulation, clotting being much slower in a smooth deep vessel than in a rough shallow one.

The **Extractives** of the blood are fats, cholesterin, lecithin, creatin, urea, hippuric acid, uric acid, and grape sugar, all in small and varying quantities. Fats occur as neutral fats, olein, stearin, and palmitin; the peculiar fat lecithin occurs only in very small proportions. The amount of fat in the blood during digestion is ·4 to ·6 per cent.; in fasting animals, ·2 per cent.; in dogs fed on a fatty diet it may reach 1·25 per cent., and may give the serum a milky appearance. There is twice as much fat in the serum of recently fed horses as in the serum of those kept starving. Other extractives such as soaps are found to the extent of ·05 to ·1 per cent.; urea, ·02 to ·04 per cent.; sugar, ·1 to ·15 per cent.

The characteristic **Difference between Arterial and Venous Blood** is that the former contains more oxygen and less carbonic acid, though there is always, in fully arterialised blood, about twice as much carbon dioxide as there is of oxygen (see p. 24). Arterial blood also contains more water, fibrinogen, extractives, salts, and sugar, fewer blood-corpuscles, and less urea; its temperature is, on the average, 1° C. lower. The dark colour of venous blood is not due to the greater amount of CO_2 it contains, but to the diminution of oxygen in the red blood-cells. The alteration in colour effected by the addition of reagents and gases to blood is probably due partly to alterations in the shape of the corpuscles themselves, which become more concave on the addition of oxygen and less concave on its removal, and also to the fact that oxy-hæmoglobin is brighter in colour than reduced hæmoglobin.

The **Salts** of the blood are divided between the plasma and the corpuscles. The distribution of these is not the same in all animals; in the horse and pig, for example, sodium only exists in the plasma and none in the corpuscles, whereas in the ox and dog both corpuscles and plasma contain it. Sodium chloride is the most abundant salt of the blood, potassium chloride and sodium carbonate come next, and lastly phosphates of calcium, magnesium and sodium. The chief inorganic substance of the cells is potassium phosphate. Iron is found in hæmoglobin but not in the plasma. The following table from Bunge bears on the question of the salts of the blood in different animals:

	1,000 *grammes of Corpuscles contain*			1,000 *grammes of Serum contain*		
	K.	Na.	Cl.	K.	Na.	Cl.
Horse	4·92	0	1·93	·27	4·43	3·75
Ox	·747	2·093	1·635	·254	4·351	3·717
Pig	5·548	0	1·504	·273	4·272	3·611

The use of the salts is to assist in secretion, repair, and disintegration. The growth of the solid tissues of the body absolutely depends on the inorganic material supplied by the blood. Water free from salts is destructive to protoplasm; no doubt, therefore, one important function of the salts in the blood is to maintain the vitality of the tissues. Sodium chloride is here especially valuable, and its extensive presence in blood (60 per cent. to 90 per cent. of the total amount of ash) corresponds to its importance. As the blood is simply the carrier of the salts, and the only means by which the tissues can obtain them, it by no means follows that all the mineral matter found in it is essential to its own repair and constitution.

The **Temperature of the Blood** in the different domestic animals varies from 100° F. to 105° F. (37·8° C. to 40·54° C.), the warmest blood in the body being found in the hepatic veins.

The **Quantity of Blood in the Body** cannot be determined by mere direct bleeding alone. After all the blood is drained off, the vessels require to be washed out, and the quantity of blood in the water estimated by the colour present; the body has then to be minced and macerated, and the quantity of blood in this estimated by the colour test, comparison being made with a standard solution of blood.

By Haldane and Lorrain Smith's carbon monoxide process the amount of blood in the living animal may be calculated. The essential steps in this process are to estimate first colorimetrically the percentage of hæmoglobin in the blood, and then the extent to which this is saturated by breathing a measured volume of carbon monoxide. In this way the total capacity of the blood for carbon monoxide may be ascertained, and the carbon monoxide capacity being the same as the oxygen capacity, the volume of the blood may be readily calculated.

Sussdorf * puts the proportion which the weight of the blood bears to the body weight as follows:

Horse - $\frac{1}{15}$ = 6·6 per cent. of the body weight.
Ox - $\frac{1}{13}$ = 7·71 ,, ,, ,,
Sheep - $\frac{1}{12}$ = 8·01 ,, ,, ,,
Pig - $\frac{1}{22}$ = 4·6 ,, ,, ,,
Dog - $\frac{1}{11}$ to $\frac{1}{18}$ = 5·5 to 9·1 per cent. of the body weight.

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* Ellenberger's 'Physiologie der Haussaugethiere.'

The same observer gives the amount of blood in the body of the horse at 66 lbs., or nearly 50 pints.

The Distribution of Blood in the Body (Fig. 8) is believed to be as follows:

About one-fourth in the heart, lungs, large vessels, and veins.
" " liver.
" " skeletal muscles.
" " other organs.

It is probable that in the horse the liver would contain less than one-fourth the bulk of blood, while the skeletal muscles would contain more. Under certain conditions the abdominal veins are capable of containing the whole of the blood in the body. When an organ is active it receives more blood than when in a state of rest; this increase has been variously estimated at from 30 to 50 per cent.

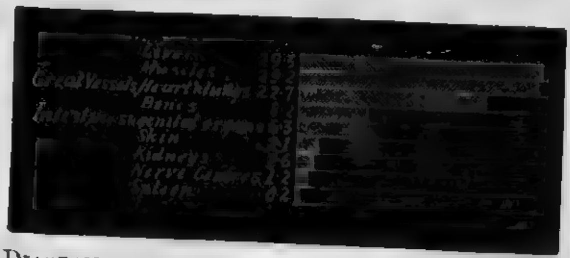


FIG. 8.—DIAGRAM TO ILLUSTRATE THE DISTRIBUTION OF THE BLOOD IN THE VARIOUS ORGANS OF A RABBIT, AFTER RANKE'S MEASUREMENTS (STEWART).

The numbers are percentages of the total blood.

The Gases of Blood.—The blood gases are obtained by introducing the fluid into a Toricellian vacuum, the instrument used to obtain it being a mercury pump. In a vacuum the blood froths up and gives off its gases, which are then collected and analysed.

The gases are oxygen, carbon dioxide, and nitrogen. The proportion of these found depends upon whether the blood be taken from an artery or a vein; in the former the oxygen is present in larger amount than in the latter, and the carbon dioxide is less. The nitrogen is in both cases practically the same.

At a pressure of 30 inches (760 mm.) of the barometer and a temperature of 32° F. (0° C.), the following gases are found in 100 volumes of blood :

	Arterial.	*Venous.*
Oxygen	20	12
Carbonic acid	40	45
Nitrogen	2	2
	62	59

The exact amount of gas varies ; the above can only be taken as convenient averages.

Oxygen exists in arterial blood in the proportion of about 20 per cent. per volume of the blood, whilst in venous blood it is found to vary within wide limits, depending upon the vessel from which it is taken, and the activity of the part at the time of its collection. In the blood of asphyxia it is nearly absent.

It will be remembered that by far the greater part of the oxygen was stated to be in combination with the hæmoglobin of the red blood-corpuscles ; in fact the proportion of oxygen in the blood bears a definite relation to the amount of iron contained by the hæmoglobin. It has been determined that 15½ grains (1 gramme) of hæmoglobin are capable of absorbing ·095 cubic inch (1·55 c.c.) of oxygen. Whatever oxygen the serum of blood contains is simply absorbed ; the amount held in solution is therefore small. Oxygen chemically united with hæmoglobin is quite independent of the laws which regulate the absorption of gases (see Respiration).

Besides the vacuum of the air-pump, various chemical substances have the power of deoxidizing the blood-cells ; such reducing substances are ammonium sulphide, sulphuretted hydrogen, some iron salts, etc. Blood exposed to the air loses oxygen, due to the production of reducing substances formed as the result of decomposition.

The **Carbon Dioxide** in arterial blood is about 40 per cent. ; in venous blood it varies, depending on the vessel from which the blood is drawn. The CO_2 is principally combined with the sodium carbonate in the plasma of the blood, though Bohr considers the hæmoglobin is also a carrier.

The **Nitrogen** in the blood is small in amount, about 2 vols. per cent.; it does not vary in arterial or venous blood, as in both cases it is simply absorbed by the plasma.

Composition of the Blood.—Reviewing the various analyses which have been published of the blood of animals, the following represents the average composition of the fluid:

The Plasma.

Water	90 parts per cent.
Proteids	8 or 9 parts.
Fats	·1 ,,
Extractives	·4 ,,
Salts	·8 ,,

The Corpuscles.

These represent from one-third to half the weight of the blood and consist of:

Water	64 parts per cent.	
Solids	35 ,,	consisting of 32 per cent. hæmoglobin, ·1 per cent. proteids.
Salts	1 ,,	

Taking the blood as a whole the following represents approximately its composition in every 100 parts:

Water	81 parts.		
Solids	19 ,,	Hæmoglobin	13 parts.
		Proteids	4 ,,
		Salts	1 ,,
		Extractives	·6 ,,

Defensive Mechanisms of the Body.—If the serum of one animal be injected into another of a different species, it may cause the corpuscles to break up (*hæmolysis*) and hæmoglobin to appear in the urine. This destructive effect is found to occur whether the blood be injected into the circulation, or merely added to the foreign blood *in vitro*. The action is termed *globulicidal*, and it can be abolished by previously heating the added serum to 132° F. (55° C.). Not only will the serum of one blood destroy the corpuscles of another, but it will also destroy certain bacteria (*bacteriolysis*), and the effect on these is greatly increased, if the animal furnishing the serum has previously been treated with an intravenous injection of similar bacteria. These facts have opened a field of therapeutics still in its infancy and endowed with great possibilities.

The substance produced in the blood which acts as a protective is known as an *antibody*; it is a defensive mechanism of the greatest importance. An antibody is not necessarily the result of bacterial activity, it may be produced in a blood by the injection of almost any proteid, and the serum so obtained is capable of precipitating that particular proteid from solution and no other; such a body is known as a *præcipitin*.

An animal may, by carefully graduated doses of virus, be rendered completely immune to a dose sufficiently large to kill many hundreds of unprotected animals. The blood serum of the one so protected may be employed in the treatment of others naturally infected or unprotected; such a serum may be both curative and protective, an example of which is rinderpest serum, or it may only be protective, as in tetanus.

Another defensive mechanism of physiological value is *phagocytosis*. No one can possibly doubt the difference in the resisting power to disease of 'fit' over 'unfit' animals, nor the greater protection afforded by maturity as compared with youth. These facts assure the perpetuation of the species and are probably intimately connected with this question. When referring to phagocytosis (p. 14) we stated that the thoroughness with which the phagocytes did their work depended upon the composition of the blood plasma. It would appear that it does not matter much from what source the leucocytes are derived, they are all capable of turning out equally good work if the blood plasma contains sufficient of a substance which acts upon the bacteria, and renders them more easily eaten by the leucocytes (Wright). The nature of the substance is unknown, but it would appear to act chemically on the bacteria, and render them an easy prey to the leucocytes; it does not act upon nor stimulate the leucocytes. This substance is known as an *opsonin*, and it is probable that there are several varieties in the plasma, each having its own particular microbic infection to deal with. Opsonins must not be confused with bacteriolysins, agglutinins (anti-bodies which agglutinate bacteria) or antitoxins, from which they are quite distinct.

The Blood in Disease.—The blood plays two distinct parts in disease, it is a carrier and distributer of infection to the body cells, and further it may itself undergo profound pathological change.

All the specific infective diseases of animals are spread through the body by means of the blood stream. It is true that the initial source of entry may be an allied passage—the lymph stream—but it is by means of the blood that the final and complete invasion of the body is effected. Nor does the observation apply to specific diseases only; if we take two such opposite conditions as anthrax and poisoning by arsenic, it is the blood in each case which is responsible for the distribution of the infecting agent.

The blood tissue itself may be the seat of disease; micro-organisms may live and multiply in the plasma and infect the whole body as in anthrax. Some of the organisms may be so small as to be ultra-microscopic, and in connection with this question some of the most acute and fatal infectious diseases of animals are caused by organisms of this class, of which rinderpest, foot and mouth disease, rabies, and African 'horse sickness' are examples. Still, in spite of the fact that these microbes have not been seen their existence is undoubted, the best evidence of which is that some of them are sufficiently large to be caught in the pores of a filter, leaving the filtrate sterile. Other organisms attack the blood cells, for example the important group of Trypanosomes, the malaria parasite, the organism of Texas fever, and such like. In these cases the product of red cell destruction may show itself by the discoloured urine and is evident in the tissues, for example the liver and spleen.

Compared with the red corpuscles the white are seldom affected with disease, but there are certain affections of the spleen associated with a great increase in their number.

There are other conditions affecting the blood, for instance *Purpura*, which cannot be attributed to parasitic agency. In this disease, either from defects in the blood or vessel-wall, hæmorrhage takes place into the tissues. No organ appears to be able to escape, though probably the subcutaneous and muscular tissues are the most frequent seat of the hæmorrhage.

Quite as strange and obscure is the dietetic disease of equines known as hæmoglobinuria, in which the animal in the middle of work suddenly falls paralysed, the urine becomes coffee-coloured and loaded with methæmoglobin, in consequence of the destruction of the red cells. What the destructive agent is, is at present unknown, but it is probably one of the poisonous products of proteid disintegration, which will be found dealt with in the chapter on digestion.

Blood-letting in the treatment of disease was at one time so universal that it came to be regarded as the 'sheet-anchor' of life, and animals were regularly bled in *order to keep them well.* 'Blood-letting' was killed by abuse; it is a question whether the pendulum has now travelled too far in the other direction, and the employment of a physiological means in the treatment of disease been too long neglected.

CHAPTER II

THE HEART

The blood in the body has to be kept in constant motion, so that the tissues which are depending upon it for their vitality may be continuously supplied, and also in order that the impure fluid resulting from the changes in the tissues may be rapidly and effectually conveyed to those organs where its purification is carried out.

The heart is the organ which pumps the blood over the body, not only distributing it to the tissues, but forcing it on from these back to the heart again, to be prepared for redistribution. It may be described as a hollow muscle divided into two compartments, usually known as right and left, but in quadrupeds really anterior and posterior, each compartment being divided into an upper half or auricle, and a lower or ventricle. Opening into the auricles are large veins which convey the blood back to the heart, while from the ventricles other vessels, arteries, take their origin for the conveyance of blood from the heart. The auricles and ventricles are separated by a valvular arrangement, and the two sides of the heart are separated by a muscular partition (Fig. 9).

So far the general arrangement of both right and left sides is much the same, each having to receive and then to get rid of a certain quantity of blood sent into it. But the blood sent into the right side of the heart is very different from that received by the left, and with this difference we must for a moment deal. The whole of the impure or venous blood in the body is brought into the right side of the heart for the purpose of being distributed to the lungs, where it is purified; into the left heart this arterial or purified blood is brought back from the lungs for distribution to the body. The passage of the impure or venous blood from the right side of the heart through the lungs to the left side is known as the *Pulmonic* circulation; that of the blood, thus purified, through the body and back to the right side of the heart is called the *Systemic* circulation (Fig. 10).

Mention has been made of *valves* in the cavities of the heart; they are found on both sides separating auricle from ventricle, and are known as the right auriculo-ventricular or tricuspid valve, and the left auriculo-ventricular or mitral valve. Besides these, valves are found in the vessels arising from the ventricles, viz., in the pulmonary artery and the aorta; these valves, pulmonary and aortic, are known as the semi-lunar valves. No valves are found guarding the entrance of the vessels (veins) into the auricles.

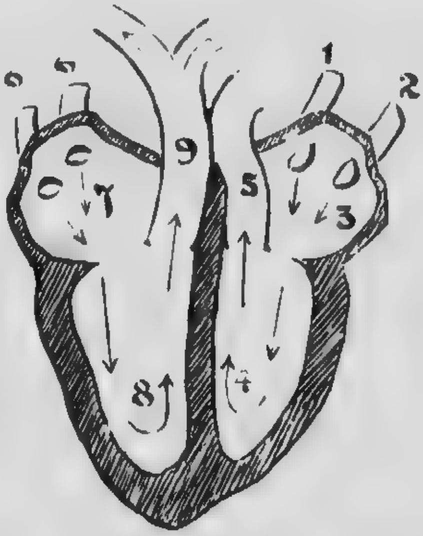


FIG. 9.—DIAGRAM OF THE CIRCULATION THROUGH THE HEART.

1 and 2, The venæ cavæ; 3, right auricle; 4, right ventricle; 5, pulmonary artery; 6, 6, pulmonary veins; 7, left auricle; 8, left ventricle; 9, aorta dividing into anterior and posterior. The arrows represent the direction taken by the blood stream.

In order to understand the function of these valves, which play such an important part in the physiology of the heart, it is necessary that we should briefly detail the course which the blood takes from the time it enters the right auricle, until it completes the round of the circulation and finds itself at this auricle again.

Course of the Circulation.—The venous blood from the whole of the body flows into the right auricle by means of the anterior and posterior venæ cavæ; it passes from here through the tricuspid valve into the right ventricle; from the right ventricle it travels to the lungs by means of the pulmonary artery, where, having been exposed to the action of the air and become greatly changed in its gaseous composition, it returns to the heart by means of the pulmonary veins, emptying itself into the left auricle. It now passes through the auriculo-ventricular opening into the left ventricle, and thence into the aorta to be pumped all over the body, being distributed by means of the arteries and capillaries; it is then collected by the veins, and eventually brought back to the heart to undergo afresh its distribution to the lungs and body (Fig. 10).

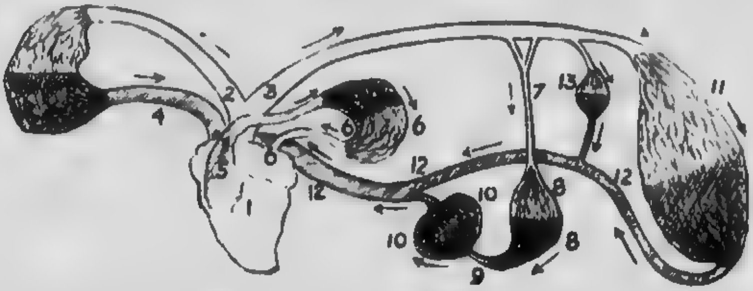


FIG. 10.—DIAGRAM OF THE CIRCULATION OF THE BLOOD.

1, The heart; 2, anterior, 3, posterior aorta; 4, anterior vena cava; 5, pulmonary artery; 6, pulmonary veins; 7, mesenteric arteries; 8, intestinal capillaries; 9, portal vein; 10, the liver, the veins from which open into (12) the posterior vena cava; 11, the circulation through the hind extremities; 13, the circulation through the kidney.

The use of the valves is to allow of and to insure the transference of blood from auricles to ventricles, and from the ventricles to the aorta and pulmonary artery without any chance of regurgitation. This they do in virtue of the fact that they are so constructed and arranged as to open only in that direction towards which the blood has to be sent.

Position of the Heart.—The heart occupies a position in the middle line of the chest, being enclosed in a sac, the pericardium, and suspended from the spine by its aortic vessels. Its base is uppermost, its apex nearly touches the sternum, and the organ occupies in the horse a position corresponding to the third, fourth, fifth, and sixth ribs. It is between the fifth and sixth ribs, at their sternal insertion, where the *impulse* or 'beat' of the heart may be felt in the horse. Its other relations are with the diaphragm which is just behind the apex, but with which it has no structural connection. On its right side is the right lung, and on its left part of the left lung; there is a triangular notch in the left lung of the horse which exposes the left ventricle, and allows it to make its impulse felt against the chest wall. The anterior face of the heart is formed by the right auricle and ventricle, the posterior by the left auricle and ventricle.

Heart Muscle.—The heart is an involuntary muscle, but does not conform histologically to the involuntary muscular fibres met with in other parts of the body. The muscle is red in appearance; microscopically its fibres are short, striated both in a cross and longitudinal direction, possess no sarcolemma, and anastomose freely. The network formed by the fibres of the heart is a most distinctive feature of cardiac muscle. The contractile tissue, though spoken of as a fibre, is in reality a quadrilateral nucleated cell. In some animals, sheep and ox in particular, cells of a peculiar kind are found immediately beneath the endocardium; they are polyhedral in shape, containing protoplasm and a nucleus, and are surrounded by striated fibres; they are called the *cells of Purkinje.*

The arrangement of the fibres of the heart is peculiar; the fibres of the auricle are quite distinct from those of the ventricle, and both are arranged in layers. Two layers exist in the auricle, circular and longitudinal, the circular fibres being continued around the entrance of the veins, whilst in the ventricle several layers exist of oblique, longitudinal, and circular fibres. Owing to the peculiar direction in which the oblique fibres run a somewhat spiral arrangement results. It has been shown that the auricles and ventricles, though separated by a fibrous ring, are yet connected by bands of altered muscular tissue which pass through the ring.

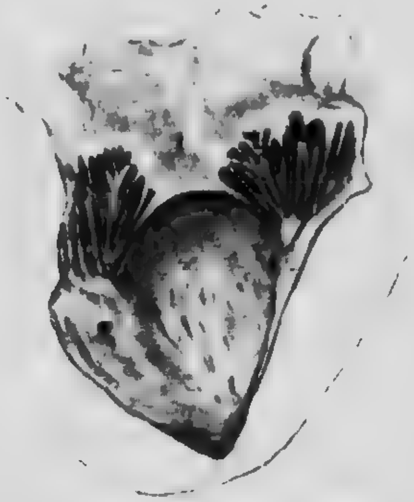


FIG. 11.—LEFT VENTRICLE OF HORSE EXPOSED TO SHOW MITRAL VALVE.

1, Portion of valve; 2, *columnæ carneæ*, on the upper surface of which are found the *musculi papillares*, to which the *chordæ tendineæ* are attached.

The cavities of the heart are lined by the endocardium which is reflected over the valves; this membrane in the left auricle of the horse is of a peculiar grey colour.

Certain fibrous rings are found in the heart where the valves are situated, and to which these obtain a firm attachment. The ring surrounding the aortic opening in the ox has constantly in its substance one or more pieces of bony tissue; this is also common in the horse.

Valves of the Heart.—The *auriculo-ventricular* valves are made up of fibrous membrane, in which a small proportion of muscular fibre is found close to the attached border. The *mitral* or *bicuspid* valve in the horse consists of one large distinct segment, and several smaller ones united to form a second; the tricuspid consists of three segments, one, much larger than the others, being placed opposite to that portion of the ventricle which leads to the pulmonary artery.

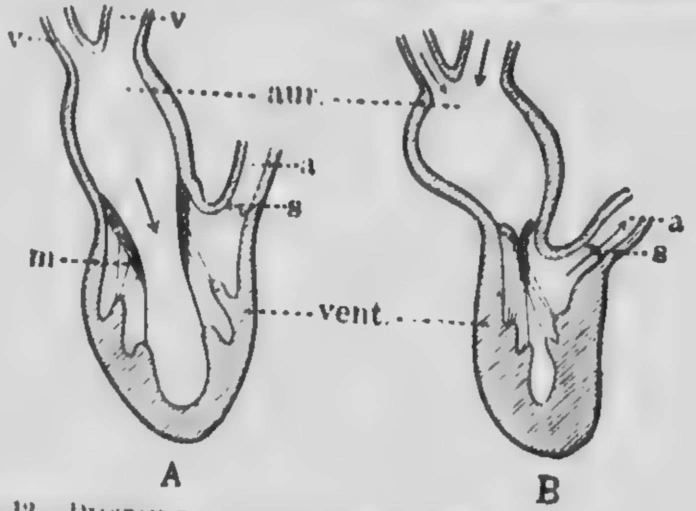


Fig. 12.—Diagram to illustrate the Action of the Valves of the Heart (Huxley).

In A the auricle is contracting, ventricle dilated, mitral valve open, semi-lunar valves closed. In B the auricle is dilated, ventricle contracting, mitral valve closed, semi-lunar valves open. *Aur.*, auricle; *vent.*, ventricle; *v.*, *v.*, vein; *a.*, aorta; *m.*, mitral valve; *s.*, semi-lunar valve. Note the manner in which the papillæ have shortened in B, in order to compensate for the ventricular walls approximating.

The free edges of all the valves are held in position by large and small tendinous cords (*chordæ tendineæ*) composed of fibrous tissue, which are inserted into *musculi papillares* found on the internal surface of the ventricle; the cords from one papilla do not all pass to one segment of the valve, but to two or three (Fig. 11). The function of the papillæ is to restrain the valves from flapping back into the auricle during the contraction of the ventricle, and this they accomplish by gradually shortening as the walls of the ventricle approximate; compensating by their shortening for the movement of the ventricular wall and thus exerting traction on the cords (Fig. 12). Other bands pass from one side of the ventricle to the opposite wall; they are called *moderator bands*, and their function is to restrain the ventricular wall from undue distension.

The valvular flaps meet in the most perfect apposition when the ventricles contract, their edges are inverted, and the sides of the valves curl in and lie so close to their fellows that nothing can escape upwards into the auricles (Fig. 13). This may be readily demonstrated in the dead heart by tying the aorta and pulmonary veins, and introducing into the left auricle a tube which admits a powerful jet of water; the left side of the heart distends and hardens, and at last water forces its way out of the hole in the auricle through which the tube is inserted. If the auricle be now opened, the ventricle is found cut off from view by a tense membranous parachute-like dome, convex towards the auricle, which is the mitral valve in position; not a drop of water will escape from the ventricle, though the heart be turned upside down, and it requires some little force to depress the valve.

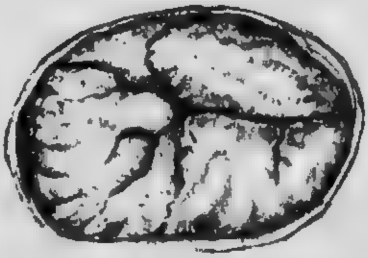


FIG. 13.—TRICUSPID VALVE IN CLOSED POSITION SEEN FROM THE AURICLE.

Note the cracks in the surface, which represent where the margin of the valves meet and fold in against each other like the lips of a toothless mouth.

The semi-lunar or sigmoid valves, which guard the entrance into the aorta and pulmonary artery, are composed of fibrous tissue, and possess at the centre of each segment a small hard body, *corpus Arantii*, which is particularly marked in the aorta.

Movements of the Heart.—If the exposed mammalian heart be watched at work, a great deal may be learned of its action. It will be observed that both auricles contract together and both ventricles together; further that certain changes in shape occur. The contraction of either auricle or ventricle is spoken of as its **systole**, while the subsequent relaxation is described as its **diastole.**

Prior to any heart movement occurring the roots of the veins entering the auricles contract through the medium of the circular fibres surrounding them; this contraction next sweeps over the auricles which are drawn downwards towards the ventricles, the auricular appendage taking an active part in expelling its contents. The ventricles then contract, but more slowly, and as they do so they shorten, become more circular in shape and owing to the oblique direction of the muscular fibres above described, there is a twisting or squeezing of the ventricular walls. The contraction of the ventricles does not begin at the apex, as might be supposed, but at the base, and extends from there to the apex. Further, there is no apex beat, for the apex does not move unless the pericardium be opened.

The contraction of the ventricles is succeeded by a *pause*, during which the heart is in a state of relaxation.

A **Cardiac Cycle** is the term used to describe the changes which occur in the heart, during the time which elapses between one contraction or relaxation of the auricle, and the one which immediately succeeds it.

We may take the moment when the blood is entering the auricles from the venæ cavæ and pulmonary veins as the most convenient point to start from. This flow is brought about by the pressure of blood in the veins, which though low is yet higher than that in the auricles. Further, the flow into the right heart is assisted by gravity, particularly the blood in the anterior vena cava, while even in the posterior vena cava this is by no means a negligible quantity. There is likewise an aspiration in the veins produced by a relaxation of the walls of the auricle after the previous contraction, and an aspiration in the thorax the result of inspiration, which gives rise to a negative pressure in the veins leading to the heart (see p. 91).

The auricles being now full, a wave of contraction which first appears at the vessels leading into them, passes over these chambers, which by a sudden sharp and brief contraction empty their contents into the ventricles. The systole of the auricle produces a backward positive wave in the vessels leading into it, and this wave passing through the anterior vena cava, shows itself in the jugulars of the horse by a distinct pulsation at the root of the neck.

The auricular contraction forces the blood into the ventricles, which have been partly filling during the time the auricles were distending, and the final filling of the ventricle by the auricular systole forces up the auriculo-ventricular valves, which bulge into the auricle under the increasing pressure to which the ventricular contents are exposed. The ventricles give a prolonged contraction, and owing to the spiral arrangement of their muscular fibres exhibit a peculiar movement. The pressure which now exists in the ventricles is greater than that in the vessels leading from them, and as the auriculo-ventricular valves cannot be thrown open upwards into the auricles owing to their chordæ tendineæ, the semi-lunar valves are forced open, and the stream of blood passes into the aorta and pulmonary artery. At the moment the ventricles contract, the heart slightly rotates around its vertical axis from left to right, while the left ventricle hardens and makes its impulse felt against the chest wall. The impulse is synchronous with the closure of the auriculo-ventricular valves, and the forcing open of the sigmoid valves. The systole of the ventricle produces a dull, booming, prolonged sound, which is brought about by the muscular contraction of its walls, and probably, at the same time, partly by a vibration of the auriculo-ventricular valves; the sound is known as the *first sound of the heart*.

The blood now rushes into the aorta and pulmonary artery, and the elastic resistance of these arteries being brought into play, the fluid has a tendency to regurgitate towards the ventricles; by this process the semi-lunar valves are closed, the closure being accompanied by the *second sound of the heart*, which is short and sharp. This sound is due to the sudden tension of the membranous flaps of the valves at the moment of their closure, which gives rise to vibrations.

The semi-lunar valves are mechanically most perfect. The thin margins on either side of the *corpora Arantii* are closely pressed together, the corpora Arantii filling up the centre, and not a drop of blood passes back into the ventricles. These valves do not lie back close against the arterial wall during the exit of blood from the ventricle, but stand out in the stream, probably being kept there by reflux currents. They form a triangular orifice with curved sides.

The arterial trunks which during the systole of the ventricles elongate and curve, now at the diastole shrink and shorten, and so bring the base of the heart back to its former place. The force of aortic reflux is not wholly expended on the valves, but largely on the muscular pads to which the valves are attached; to admit of this the diameter of the aorta is much greater than the opening out of the ventricle.

It is not until the semi-lunar valves are firmly closed that the ventricles begin to relax; this they now do, and the relaxation of the walls produces a negative pressure, viz., a pressure below that of the atmosphere, which in the dog has been measured at from 1 to 2 inches (25 to 50 mm.) of mercury. This negative pressure opens the auriculo-ventricular valves, the blood flows in from the auricle, while the auricle and ventricle, neither contracting nor dilating, assume a passive condition during a period known as the **pause**. Throughout the pause blood is flowing into the auricles from the pulmonary veins and venæ cavæ, and into the ventricles from the auricles; towards the close of the pause the auricles contract, and the whole process is repeated.

We have thus the contraction of the auricles, the contraction of the ventricles, and the pause. The time each of these occupies has been determined for the horse, by Chauveau and Marey, by means of a cardiac sound. The value of the periods they give us is as follows: auricular systole, two-tenths of a second, ventricular systole, four-tenths, and pause, four-tenths of a second. We cannot accept the value of these periods as correct, owing to the fact that they cause the horse to have a pulse of 60 to the minute, which is distinctly abnormal; 36 to 40 beats per minute is the normal rate.

A complete cycle of the horse's heart occurs, on an average, once in every 1·5 seconds; but the time value of the various phases which make up this period cannot be exactly stated. No matter how fast the heart is beating, the frequency depends not on the duration of the ventricular systole, but on the length of the subsequent pause.

Summary of Events occurring during a Cardiac Cycle.—Dividing the events into three periods, and starting with the contraction of the auricles, the following is a summary of the changes occurring in the heart:

1*st Period.*—The contraction of the auricles completes the filling of the ventricles.

2*nd Period.*—The ventricles contract, the auriculo-ventricular valves are closed, the aortic and pulmonary valves open, blood is pumped into the aorta and pulmonary artery, the impulse of the heart is made against the wall of the chest, the first sound is produced, the auricles fill with blood, and the whole is followed by a short pause.

3*rd Period.*—The aortic and pulmonary valves close, the auriculo-ventricular valves open, the second sound of the heart is produced, diastole of both auricles and ventricles occurs, followed by a long pause, during which blood flows into all the chambers.

The impulse of the heart, to which we have previously referred as being felt externally between the fifth and sixth ribs, is not given by the apex, but by the lower half of the left ventricle. There is no such thing as an apex beat;

the apex practically does not move as long as the heart is retained within the pericardium, but if the latter be opened, the apex is tilted forward with each contraction. The **Use of the Pericardium** is to prevent over-distension of the heart.

The **Action of the Valves of the Heart** during a cardiac cycle is peculiar and interesting. We have described how the auriculo-ventricular curtains are floated up as the ventricles fill, and how with increased pressure they come together, being prevented by the chordæ tendineæ, and the muscular pillars to which these are attached, from being pushed back into the auricle. Further, experimental inquiry has determined that when the ventricular systole is at its height, these valves bulge upwards into the auricles, assuming a concave surface towards the ventricle; this appears to be especially the case in the horse.

The pulmonary valves, and probably the aortic, not only meet at their free border but actually overlap. Chauveau states that he has tried experimentally to hold back one of the pulmonary valves, but the others have applied themselves so closely around the finger that it was impossible to produce a patent opening. In the aorta it is probable that overlapping does not occur to the same extent, and here the corpora Arantii are of value. When the sigmoid valves are not acting they still lie in the blood stream, and not against the wall of the vessel as was at one time supposed; nor do those in the aorta cover the openings of the coronary arteries.

It is generally believed that both the aortic and pulmonary valves are closed by the regurgitation of the blood; but it has been pointed out that as the blood is leaving both ventricles, it is streaming through orifices which at that time are mere chinks, owing to the pads of muscle which take their origin from all sides of the mouth of the vessels. Vortices are thus created in the space between the arterial root and the edge of the valves. These vortices tend to press the edges of the valves together, and the valves consequently close the moment the blood actually ceases to stream through the narrow crevice. In this way there is no regurgitation, as the valves are closed before the recoil of the aorta. If this explanation be correct, the second sound of the heart must be considered as due to the sudden *tension*, and not the closure, of the aortic valves at the time of the aortic recoil.

The **Cardiac Sounds** are really four in number, but as they are in pairs we recognise only two. The first sound is a long booming one, due to the muscle-sound of the contracting ventricle, assisted, probably, by the simultaneous vibrations of the auriculo-ventricular valves. The second sound is due to the sudden tension of the aortic and pulmonary valves at the moment of their closure, which gives rise to vibrations. It is a short sound, and its source has been clearly proved by hooking back the valves, which causes the sound to cease. The two sounds are reproduced by the words '*lubb dŭpp.*'

Intra-Cardiac Pressure.—The internal pressure exercised by the walls of the heart on the blood, is ascertained by means of an instrument termed a cardiac sound, first used by Chauveau and Marey. It is a double tube having at its extremity two elastic balls; the air in these is compressed when the cavities contract, and the compression moves a lever placed in connection with a recording surface. The instrument is passed into the right heart through the jugular vein, one ball being in the auricle, the other in the ventricle. It is stated that its presence causes no inconvenience to the animal, due to the fact that no sentient nerves are supplied to the lining membrane of the blood-vessels or even to the heart. A tracing so obtained from the heart of the horse is shown in Fig. 11: the curves do not indicate the force of the stroke, but only the differences in intra-cardiac pressure at each instant of one contraction. It is seen from the tracing that the auricles contract first, followed by the ventricles. The contraction of the former is sharper and shorter than of the latter, which is slower, maintained for some time, and then falls.

Observations on the intra-cardiac pressure show that it is greatest at the beginning of contraction, and then gradually falls; whilst a negative pressure occurs during the period of diastole, and is brought about by the relaxation of the walls of the heart during the long pause. This relaxation causes a sucking action which assists in filling the heart with blood.

Though both ventricles deliver the same amount of blood the pressure in each cavity is different, owing to the differences in the resistance to be overcome in the systemic and pulmonic circulations. The systolic pressure in the left ventricle of the horse is equal to a column of blood from 9 to 14 feet (2·4 to 4·3 metres) in height, or 178 to

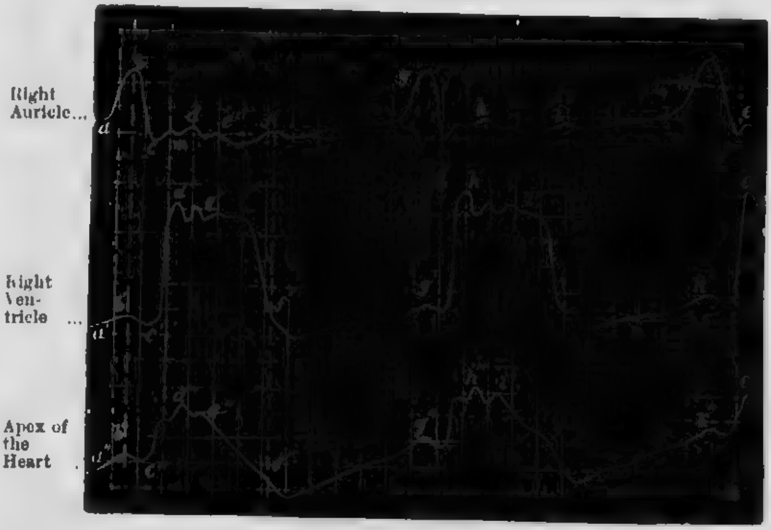


FIG. 14.—SIMULTANEOUS TRACINGS FROM THE INTERIOR OF THE RIGHT HEART OF THE HORSE, AFTER CHAUVEAU AND MAREY (M'KENDRICK).

Each horizontal line equals $\frac{1}{10}$ second, the vertical lines indicate pressure; the vertical dotted lines mark coincident points in the three movements.

The auricular curve is *a*, *b*, *c*, the ventricular curve is *c'*, *d'*, *e'*, *f'*. The auricle contracts sharply, relaxes rapidly, and is followed by the contraction of the ventricle which is maintained with certain oscillations for about three-tenths of a second, and then relaxes; the pause follows at *f*, *f'*.

The oscillations seen at *d*, *d'*, *d''*, and *e'*, *e'*, *e''*, are believed to indicate vibrations of the tricuspid valve.

318 mm. of mercury, and in the right ventricle is equal to 1½ feet of blood (·46 metre), or 34 mm. of mercury in height. In the dog the intra-cardiac pressure has been estimated as follows:

Left ventricle - -	7 inches	(180 mm.)	of mercury.
Aorta - - - -	6¼ „	(160 mm.)	„
Right ventricle - -	1¾ „	(45 mm.)	„

The Cardiograph.—The impulse of the heart against the chest wall is graphically obtained by means of the cardiograph, of which there are many forms. Their essential construction consists of a button applied externally to the chest wall, which is pressed upon by each impulse of the heart, and so conveys the movement to an elastic air-chamber, which transmits it to a recording lever. By this means we obtain a graphic representation of the heart's impulse, but there are many difficulties in obtaining reliable records with this instrument.

The cardiograph demonstrates that the aortic valves close slightly before the pulmonary.

Capacity of Heart.—The quantity of blood in the heart can only be ascertained approximately; measuring the capacity of the chambers is no guide. Munk states that the capacity of the ventricle in a horse weighing 880 lbs. is about 1·76 pints (1 litre), equivalent to 2·25 lbs. (1 kilo) of blood; each ventricle contains one-thirtieth of the total blood, so that when both contract one-fifteenth of the total blood is ejected. Colin gives the capacity of the left ventricle of the horse at 1·76 pints, and states that at each systole two-thirds or three-fourths of this quantity are injected into the aorta, viz., 1·17 pints (670 c.c.) to 1·36 pints (772 c.c.); the left ventricle at each contraction, according to this observer, forces into the aorta about one-twenty-fifth of the total blood of the body. It is said by Colin, that in the horse the ventricles do not empty themselves completely at each systole, and this appears to be the case in all animals.

Each side of the heart must hold the same quantity of blood, for it is evident the amount of blood leaving the heart must be equal to the amount entering it.

Work of the Heart.—This may be calculated if we know the amount of blood being discharged from the heart at each stroke, and the pressure against which it is propelled. The amount pumped out at each systole of the ventricle is liable to great variation, at least such are the results of experiments on the dog. It is obvious that the right ventricle does less work than the left, for the reason that it has to pump the same volume of blood against a much smaller *peripheral resistance*; it has been said indeed that the right heart does one quarter the work of the left.

If we take the amount of blood pumped at each stroke into the aorta of the horse at about 2·25 lbs. (1 kilo) in weight, and the pressure under which it is forced upwards as equivalent to a column of blood 10 feet in height, then the work of the left ventricle at each stroke is equal to 22·5 lbs. raised one foot high, or for 24 hours, allowing the work of the right heart to be one-fourth that of the left, 1,539,000 foot pounds. This amounts to about one-thirtieth of a horse power per diem; Munk places it at one-thirty-sixth of a horse power. If the amount of blood expelled by the left ventricle at each stroke be equal to 2·25 lbs., then in a state of repose the entire blood in the body of a horse passes through the heart in about thirty beats, or in 45 seconds. Munk says that in the horse the entire blood passes through the heart in 50 seconds, in the ox in 40 seconds, and in the dog in 20 seconds.

Since the amount of work performed by the heart is increased during exercise, the above calculations are for a horse in a state of repose.

The term **Blood Pressure** is frequently used in the physiology of the circulatory system. It is one we shall have to consider in detail when we come to speak of the bloodvessels; but it should be clearly understood that the condition is due to the amount of blood pumped into the vessels by the heart, and the pressure which results from this depends principally on the rate at which that which is in front of it in the vessels escapes into the veins. If the arterioles are contracted so that the amount passing into the veins is reduced in quantity, then a larger bulk of blood will be between the pump and its outlets, and the blood pressure rises; if, on the other hand, the blood is passing rapidly through the relaxed arterioles into the veins the blood pressure falls. When the amount poured into the venous system in any given time is equivalent to that pumped into the arterial system during the same time (which is the normal condition), the pressure is described as being constant.

The above facts may be tabulated as follows:

When the heart is more active the blood pressure rises.
,, ,, less ,, ,, ,, falls.
When the arterioles contract the blood pressure rises.
,, ,, dilate ,, ,, falls.

The heaviest work the heart performs is in overcoming the resistance offered by the minute bloodvessels or arterioles; only a very small part of the heart's work is expended on producing blood velocity. This question of peripheral resistance will shortly be considered in detail.

The **number of heart beats** in different animals, and the conditions influencing it, are more conveniently considered in the next chapter, see p. 70.

Nervous Mechanism.—The heart is said to possess no sensory nerves; it may be handled, pinched, pricked, or otherwise injured without provoking the least sign of pain on the part of the animal. Colin's experiments in this direction on horses appear quite conclusive. Not only is it considered that the external surface is insensible to pain, but the internal surface also; for, as previously noted, the experimental introduction of foreign bodies into the cavities of the heart appears to produce no pain. Under pathological conditions the results are otherwise; foreign bodies, so common in the heart of the cow, cause great suffering, therefore, there must be sensory nerves, though normally their excitability is probably low.

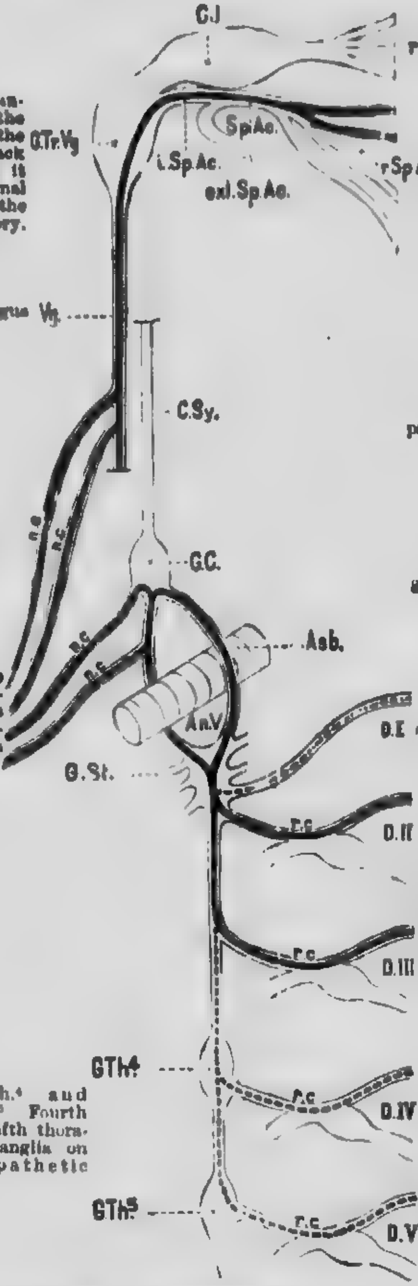
The nerves supplying the heart are the pneumogastrics, or vagus nerves, and the sympathetics; the function of these is diametrically opposite. The pneumogastric has a restraining, or, as it is termed, *inhibitory* effect over the movements of the heart; the sympathetic has an *accelerating* or *augmenting* effect. Histologically the two nerves differ greatly in structure, the pneumogastric being a medullated, whilst the sympathetic is a non-medullated nerve.

The inhibitory fibres found in the vagus are derived from the internal branch of the spinal accessory, which joins the vagus within the skull, and travelling with this nerve reaches the heart by its cardiac branches. The accelerator nerves arise from the spinal cord, by the inferior roots of the second and third dorsal nerves and probably of others; they pass through the sympathetic ganglia, and reach the inferior cervical ganglion, from which they are distributed to the heart. (See Fig. 15.)

If the **Vagus Nerve** in the neck be gently stimulated the *rate of the heart beat* is slowed and the *force of the beat* reduced. Either of these effects may occur, or they may be combined. If instead of stimulating gently a strong stimulation be applied, the heart stops in diastole. Strong stimulation may be applied to the vagus of the cat without stopping the heart, but in the dog even weak stimulation may cause it to cease beating.

The above action of the vagus is spoken of as *inhibitory*; it controls or inhibits the heart beat. Experiment shows that while both auricles and ventricles are affected by this action of the vagus, yet the effect appears to be more marked upon the auricles than on the ventricles. The effects of the vagus on the heart are often better demonstrated through one nerve, frequently the right, than its fellow, and this is explained by saying there are more inhibitory fibres in one nerve than in the other.

If one vagus be cut the rate of the heart beat is slightly increased, if both be cut the rate is greatly increased, and the blood pressure rises; the reason why the beats are in-



G.Tr.Vg. Ganglion on the trunk of the vagus; the black line through it is the internal branch of the spinal accessory.

Inhibitory fibres from spinal accessory entering the vagus.

Vg. The vagus.

C.Sy. The cervical sympathetic nerve.

G.C. Inferior cervical ganglion.

Asb. Subclavian artery.

nc., nc. The cardiac branches of the vagus conveying inhibitory fibres to the heart.

An.V. Annulus of Vieussens.

G.St. Ganglion stellatum.

D.II., D.III. The inferior roots of the second and third spinal nerves, passing by means of r.c. the ramus communicans to the ganglion stellatum. These are the augmentor fibres, passing both by the annulus and inferior cervical ganglion to the heart by nc, nc.

G.Th.4 and G.Th.5 Fourth and fifth thoracic ganglia on sympathetic chain.

The dotted line in certain thoracic nerves, D.I., D.IV., and D.V., indicate that they may contribute augmentor fibres to the sympathetic.

FIG. 15.—DIAGRAMMATIC REPRESENTATION OF THE CARDIAC INHIBITORY AND AUGMENTOR FIBRES IN THE DOG (FOSTER).

The upper portion of the figure shows the inhibitory, the lower the augmentor fibres.

creased in frequency is that the inhibitory action of the vagus is removed, and the antagonistic nerve, the sympathetic, has things all its own way. If now the cut end of the vagus be stimulated impulses are sent out which call into existence the inhibitory action, and the heart beats become fewer and more feeble.

If an artery be placed in communication with a recording apparatus and the vagus stimulated, a tracing such as that seen in Fig. 16 is obtained. The inhibitory effect is not obtained immediately the stimulus is applied; at least one beat may occur before the heart stops, and in the same way the beats do not return immediately the stimulus is withdrawn. The effect of this on the blood pressure is seen in Fig 16, where the drop in the curve is due to a fall in blood pressure the result of cardiac inhibition, while it rises by leaps and bounds shortly after the stimulus is withdrawn.

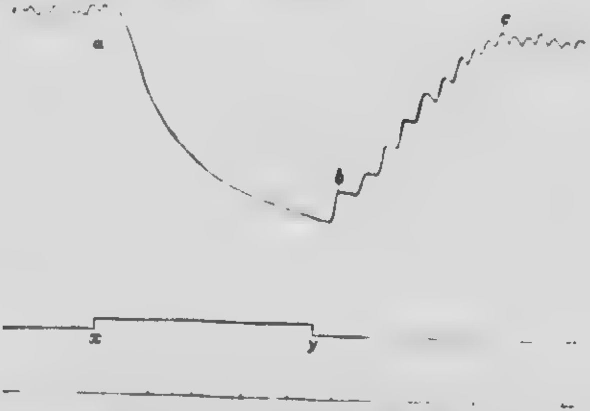


FIG. 16.—TRACING SHOWING THE INFLUENCE OF STIMULATING THE VAGUS NERVE; FALL OF BLOOD PRESSURE DUE TO ARREST OF THE HEART. FROM A RABBIT (FOSTER).

x marks on the signal line when the current is thrown into, and *y* shut off from the vagus. The time marker below marks seconds. *a* corresponds in point of time with *x*; the heart does not at once cease to beat. The first beat *b* occurs a short time after shutting off the current. The notches in the tracing are the beats of the heart.

The inhibitory power of the vagus is lost if *atropin* be applied to the heart or injected into the circulation, owing to its nerve endings in the heart being paralysed. Minute doses of this alkaloid are sufficient to prevent stoppage of the heart's beat by stimulation of the vagus. The action of atropin is counteracted by *muscarin* or *physostigmin*, both of which produce a remarkable slowing effect on the heart, even causing it to stop, behaving, in fact, very much like vagus stimulation.

The inhibitory action of the vagus on the heart is under the control of a centre in the medulla; the exact extent and position of this is not known, but it is situated close to the origin of the vagus. The centre is spoken of as the *cardio-inhibitory*, it is bilateral, and from it the inhibitory fibres which pass down the vagus obtain their origin. This centre is in action during the whole life of the animal; its constant action is known as *tonic activity*, and its function is to keep a rein on the heart; the tighter the rein is held the slower the heart beat becomes, the slacker the rein the quicker the beat. As to whether the rein shall be tight, moderate, or slack, depends upon the afferent impressions carried to the centre from the periphery, and impulses carried in this way and passed out through another channel are described as *reflex impulses*. If the central ends of sensory nerves be stimulated the heart may slow down; painful stimulation of any sensory surface, a blow on the abdomen, an accident, sudden fright, or in the human subject a sickening sight, may reflexly slow the heart through the above centre. The centre is also excited by carbonic acid, since venous blood circulating through it slows the beat. It is probable that the tonic activity of the centre throughout life is a *reflex tonus*, viz., is not due to impulses originating in the centre, but to the centre always being stimulated through a continuous inflow of sensory impressions. A rise in blood pressure causes a slowing of the beat (Marey's law), which is a good example of reflex inhibition effected through the cardio-inhibitory centre.

In the dog, cardiac inhibition is slightly increased during expiration, so that in this animal the heart beats slower during expiration than during inspiration; the effect is abolished by section of the vagi (see Figs. 18 and 19).

The **Sympathetic** nerve is the augmentor nerve of the heart; it accelerates the beat, and is consequently the antagonist of the vagus. When stimulated the rate of beat is increased, and in some cases not only the rate of beat but its force. Finally in a third group of cases the force and not the rate is increased. The explanation of these differences on stimulation is considered to be that the sympathetic contains two sets of fibres—(1) the *accelerators*, which increase the rate of beat, and (2) the *augmentors*, which produce a more forcible beat. These may act separately or in combination.

If the sympathetic nerves on both sides be cut, the heart rate is decreased owing to the influence of the uncontrolled vagus. This view of the effect of the divided sympathetics has not always existed; at one time it was held that division of the sympathetic led to no effect upon the rate of the beat, from which it was reasoned that the influence of the sympathetic, unlike the vagus, was only occasionally in operation. A centre in the medulla controls the operations of the sympathetic; it is known as the *accelerator centre*, and it is believed that, like the inhibitory centre, it is in a state of tonic and constant activity.

The two antagonistic forces above described are constantly at work on the heart: the inhibitory through the vagus slowing the rate, the accelerator through the sympathetic quickening the rate. Whichever of these effects is at any given moment most needed, is brought into play by impulses from the centres in the medulla.

The vagus is the protecting nerve of the heart. It is commonly observed after its stimulation and the consequent inhibition, that on recovery there is an improvement either in the rate or force of the heart beats. Gaskell concludes from this that inhibition is due to a building up, *anabolism*, of the muscular tissue brought about by the vagus, and resulting in an improvement in the condition of the heart. Conversely, he regards the sympathetic as a *katabolic* nerve, viz., one bringing about tissue destruction. During muscular contraction, as we shall learn later, there is a breaking down of the complex muscle elements into simpler bodies, with the production of heat and energy. In the case of the heart muscle this may be hastened through the agency of the sympathetic nerve.

The Depressor Nerve.—The nervous mechanisms considered up to this point are concerned in bringing about some modified action of the heart, under the guiding influence of a nerve centre in the medulla. We have now to consider the case where a nerve running *from the heart* to the medulla is engaged in a regulative action which, unlike that of the vagus or sympathetic, is not a direct action on the heart itself, but is brought to bear indirectly on the heart through the instrumentality of the vascular (arterial) system. This nerve is the *depressor*. It originates in the heart, some say in the walls of the aorta, and runs up the neck as a separate branch in the horse, cat, and rabbit, but in other animals it is contained in the trunk of the vagus. It joins the superior laryngeal nerve, and finally reaches a centre in the medulla which regulates the movements of the bloodvessels of the body, known as the *vasomotor centre*. The heart in this way is placed directly in communication with the centre which presides over the vascular system, a centre by whose varying activities the arteries of the body are made smaller (constricted) or larger (dilated), according to the needs of the system. If the heart is labouring and its muscular structure becoming weakened, impulses pass up the depressor to the vasomotor centre, resulting in impulses being sent out which cause the abdominal arteries to dilate and hold more blood. By this means the peripheral resistance is diminished, the blood pressure falls, and the heart is eased, since it now has less work to do in ejecting its contents.

If the depressor nerve be divided no effect follows; if the end in contact with the heart be stimulated there is no result, but if the central or upper end be stimulated, the blood pressure falls (see Fig. 23, p. 79).

Cause of the Heart Beat.—The nervous mechanisms connected with the heart, which we have just considered, only deal with the rate and force of contraction and have nothing to do with causing the rhythmical contraction; the same may be said of the nervous ganglia which are found in the substance of the heart. The proof of this is very simple, for the heart continues in cold-blooded animals to contract rhythmically when all the nervous connections are divided. Further, a strip of tissue may be so cut from the ventricular wall as to be apparently free of all ganglionic structures, and such a strip may, under suitable conditions, be made to contract automatically and rhythmically.

Accordingly, it is in some peculiarity of the muscle tissue that the cause must be sought. As the result of many observations it is laid down as an axiom that the heart is automatic, viz., that the stimulus to activity arises from within and is not brought to it from without. The nature of this *inner stimulus* cannot be regarded as solved, but it is probable that it is to be sought largely in the composition of the blood or lymph circulating through the heart tissue, and with special reference to the inorganic salts these fluids contain.

The automatic rhythmic action of the heart is most highly developed at the venous end and least so at the apex; it begins at the veins, courses over the auricles, and runs down the ventricles. Whatever may be the rhythm, the venous end of the heart sets the pace, as it is expressed, for the whole organ. The wave of contraction passes from chamber to chamber through the muscle substance, but the muscular ring between auricles and ventricles has a lower rate of conduction than the general substance of the heart wall. This fact has been utilized to explain the short pause between the auricular and ventricular contraction. Normally, the rhythm of the ventricles follows that set it by the auricles, but this may be destroyed or altered by compressing the connections between auricle and ventricle, either by specially arranged clamps or by ligature. By varying the compression complete or partial blocking of the normal rhythm occurs, so that the contractions of the ventricles become slower than those of the auricles.

The nature of the inner stimulus is, as already suggested, intimately connected with certain inorganic salts of sodium, calcium and potassium. With suitable arrangements for keeping the heart of the frog 'fed' with a fluid containing in solution chlorides of the above metals, the heart will continue beating for days, and even the mammalian heart may be thus kept alive, provided it be placed in an atmosphere of oxygen while being fed. On this diet of salts the heart finds the material for its inner stimulus. It would appear that not only will no other metals take the place of those named, but that each has a distinct rôle in the function of nutrition, calcium promoting contraction, sodium and potassium bringing about relaxation of the heart.

Heart muscle does not behave in its physiological properties the same as skeletal muscle, but possesses certain features peculiar to itself. If a piece of ordinary skeletal muscle be stimulated electrically it responds to a powerful stimulus with a big contraction, and to a weak stimulus with a small contraction. But the heart muscle when stimulated, if it responds at all, gives as big a contraction with a weak stimulus as with a strong one. The heart's motto, it has been said, is expressed by 'all or nothing.' Another peculiarity of heart muscle is that it is only capable of response to stimulation during the phase of diastole; if stimulated during systole no effect follows; this is known as the *refractory period* of the heart beat. The stimulus during diastole produces an extra contraction, but this is followed by a longer pause than usual, so that the extra beat is exactly counterbalanced.

The condition of distension of the heart cavities is an important factor in the beat. Within reasonable limits a full heart contracts more vigorously than one less full, though, if too long continued, dilatation and damage of the heart wall follow. We have learnt the provision made for correcting this, viz., the depressor mechanism, and the cardio-inhibitory centre.

Coronary Circulation.—The nutrition of the heart muscle is brought about by the blood supplied to it through the coronary arteries. Unlike any other arteries in the body, the coronaries are filled during ventricular diastole. During systole the muscular pressure on the arteries becomes higher than the pressure of the blood in the vessels, and in consequence the vessels are emptied, while during diastole they are filled. Cutting off the coronary circulation rapidly produces fatal results.

Action of Drugs on the Heart.—If *aconitin*, *muscarin*, *physostigmin*, and *pilocarpin* be applied to the heart, they cause a gradual slowing of the heart beat, and finally stop it in diastole as in vagus stimulation. This result is attributable to the stimulating effect these drugs exert on the endings of the inhibitory (vagus) nerves in the wall of the heart.

Atropin and *nicotin* increase the frequency of the heart beats, behaving very much as if the vagus were divided. In fact, if stimulation of the vagus be made after the application of atropin no inhibition follows, the nerve endings of the vagus in the heart being supposedly paralysed. If atropin be injected into the circulation the same results are obtained, including a dilatation of the bloodvessels. Atropin is able to remove the inhibitory action of physostigmin and muscarin.

Adrenalin applied to the heart augments and strengthens its beat, while if injected into the circulation it causes constriction of the vessels and a rise in blood pressure.

Digitalin reduces the frequency of the heart beat, and later excites the cardiac muscle to a stronger and prolonged systole. It is described as a heart tonic.

Pathological.

Disease of the heart of the lower animals is uncommon. It might have been thought that the horse would be exposed to this class of trouble, bearing in mind the enormous strain placed on his heart during labour, and the utter want of consideration shown by the vast majority of those who ride and drive horses. But it is not so. The hearts of horses exposed to the greatest strain seldom show any pathological change; probably the most uncommon lesions found on post-mortem examination are those affecting the heart. The heart may dilate under strain, but such dilatation when accompanied by hypertrophy is compensated, and no indication of trouble exists during life.

As evidence of the gross strain to which horses are exposed, ruptures of the heart are by no means uncommon. It is strange they are not more frequent. They probably would be but for the saving clause that degenerations of the heart substance are rare. When the heart ruptures it gives way in the auricle, where the wall is thinnest; so thin, indeed, that in certain parts of the auricle daylight may easily be seen through the tissue. It is the right and not the left auricle which suffers, showing how great is the resistance offered by the pulmonary vessels as the result of engorgement.

Valvular disease is not unknown, but so rare that probably there is no practitioner with a large experience in the examination of horses for soundness who ever thinks of examining the heart! On the other hand, irregularities in the heart's action are very common, frequently purely functional in character, unassociated with organic change, and do not interfere with the usefulness of the animal. A horse condemned for heart disease on the strength of an intermittent pulse may remain a living reproach to the practitioner.

In severe inflammatory chest invasions of the horse, the heart, but especially its sac, may become acutely affected. There are few attacks of severe pleurisy in the horse which are not associated with pericarditis, followed not only by a great thickening of the heart sac, but of more or less extensive effusion into it. The heart then becomes enveloped in a water jacket, which greatly adds to the gravity of the case. In the above acute cases the heart muscle suffers, and hæmorrhages into it are common and widespread.

In the dog the heart's action is naturally intermittent.

Foreign bodies in the heart of cattle, especially cows, are well known, and give rise to a peculiar train of symptoms. Vegetations on the valves of both the dog and pig are recognised in connection with certain infectious diseases.

CHAPTER III

THE BLOODVESSELS

The use of the bloodvessels is to distribute the blood over the body, to bring it in contact with the tissues, and return it to the heart. To accomplish this purpose there are arteries, capillaries, and veins.

The **Arteries** arise from one common trunk, the aorta, which by the process of dividing and subdividing like the branches of a tree form the arterial system. This system, measured by its total cross section, is very much larger than the parent trunk, in fact its sectional area, and hence its cubic capacity, has been estimated as several hundred times greater.

The large arteries differ somewhat in construction from the small ones. The microscope shows that while the large vessels are principally elastic the small ones are mainly muscular. This latter fact does not preclude the small vessels from exhibiting the elasticity possessed by the large ones, for muscular tissue is itself highly elastic.

This elastic property of arteries is an essential feature in their construction; it admits of a vessel stretching both in its width and length, and at the same time ensures its recovery to its original dimensions after the stretching force ceases to act. When we remember the intermittent force exercised by the left ventricle on the arteries, we have no difficulty in understanding the necessity for this elastic property. The arteries are always full, every contraction of the left ventricle, for example, in the horse during rest, throws into them one and a half pints of blood which must be accommodated, and this is provided for by the distension of their walls. For every one and a half pints of blood entering the aorta, an equal amount must pass out at the periphery, and the reduction in the diameter of the vessels brought about by the exit of this fluid is due to the elastic recoil of the arterial wall.

We shall study presently a further use of the elastic arterial wall, when we come to describe the flow of fluid through tubes.

Another essential feature possessed by arteries is their power of contractility. Just as we saw the larger arteries were principally elastic, so the smaller ones are principally contractile. This contractility or power of reducing their diameter is produced by the muscular coat previously spoken of. Though the smaller vessels possess this muscular coat, it by no means follows that they are always fully contracted; in fact special nerves exist for the purpose of supplying the needful impulses to the muscular tissue which controls or regulates the diameter of the vessels. In this way the muscular artery may be contracted or relaxed dependently upon the set of nerves brought into operation; and this movement of the smaller muscular vessels acts as a tap and regulates the blood supply to any given part of the body.

Capillaries.—The minute arteries terminate in the capillaries. It is in these vessels that the interchange between the blood on the one hand and the tissues on the other takes place, and this is rendered easy by the fact that the wall of the capillary consists simply of a very thin membrane composed of cells known as endothelial plates. It is through this wall that the exchange of material with the tissues occurs. The capillary is capable of expanding and contracting and so accommodating more or less blood as the case may be; this is brought about by the elastic nature of the membrane composing the capillary wall (for there are no nerves supplied to them), under the influence of the varying internal fluid pressure.

The size of the capillaries varies; in places such as the lungs they are relatively large, in other parts such as the skin they are very small. Their size depends upon the amount of blood which has to pass through them; in consequence they are larger during active exercise than during rest. If they be observed microscopically in the living animal, the capillaries may be seen as a network enclosing small islands of tissue. These are the areas where the interchange between the blood and tissues occurs.

The **Veins** receive their blood from the capillaries. They are thinner-walled than the arteries, and their walls collapse when empty. Though some variation exists in their structure, yet, speaking generally, they contain less elastic and muscular material than arteries, and more fibrous tissue. In certain veins, such as the venæ cavæ and those of the pregnant uterus, there is a considerable development of muscular tissue in their walls.

The venous system is larger than the arterial, and its capacity is therefore greater. The abdominal veins are capable of holding the whole blood of the body, as we see for instance at post-mortem examinations. The veins as they pass from the capillaries towards the heart become reduced in number and increased in size, and they terminate in the right auricle of the heart by means of two trunks, the united areas of which greatly exceed the aorta.

In the veins valves are found. These are well-marked in the veins of the head, neck, and extremities. The valves look towards the heart and supply a simple and essential means of ensuring the return flow of the blood along the veins to the heart. In certain places such as the bones, intestines, foot, and brain, the veins have no valves.

Veins are normally pulseless, but an exception must be made to this statement in the case of the lower extremity of the jugulars, just where they enter the chest. It is quite common in the horse to observe pulsations in these vessels for an inch or so along the neck, due no doubt to the contraction of the right auricle. It is, however, distinctly abnormal for these venous pulsations to extend a great distance up the neck. The presence of a marked jugular pulse is frequently associated with heart trouble.

Mechanics of the Circulation.—At each systole of the ventricle a certain amount of blood is forced under great pressure into an already full aorta, and imprisoned there by the closure of the aortic valves. The aorta dilates to receive this extra blood, because, owing to the friction in the smaller vessels, or, as we shall speak of it, the *peripheral resistance*, it is impossible for the amount pumped into the aorta at each systole to pass out at once at the periphery; in this way high blood pressure is produced in the arteries. The increase in the size of the aorta to accommodate this extra blood commences near the heart, and runs as a wave to the periphery; this wave is the *pulse*.

The two important points in the circulation which we have now to consider are blood pressure and pulse, and to understand these it is necessary that we should study briefly the laws which govern the flow of fluids through tubes. If water be pumped through a rigid tube or pipe, at every stroke of the pump as much fluid passes out at the farther end of the tube as enters it at the other. Between the strokes of the pump no fluid issues from the pipe, the jet is only produced at the moment the pump is in action. No more water can enter this rigid tube from the pump end than can leave it at the outlet. If now water be pumped through a *short* elastic tube, the outlet of which is in no way obstructed, the current of water through it behaves just as if it were a rigid tube, viz., a stream of water issues from the outlet during the action of the pump, and nothing more happens until the next stroke. An important alteration can, however, be made to the current through the elastic tube, by offering an obstruction at the outlet to the free passage of the water. The effect of this obstruction is that the elastic tube expands to accommodate the contents, while a stream pours from the partly obstructed outlet which no longer corresponds to the stroke of the pump, but is a continuous stream which issues so long as the pumping is continued. This continuous stream is produced by the elastic recoil of the tube keeping up the pressure which the pump imparted to the fluid, and the reason why the elastic recoil of the tube is now brought into play is owing to the partly obstructed outlet or, as we have already termed it, the *peripheral resistance.* If the elastic tube be of sufficient length, a continuous stream will issue in spite of the absence of a clamp; this is brought about by the internal fluid friction against the walls of the tube, which of course causes a peripheral resistance. In elastic tubes, therefore, the recoil of the tube converts an intermittent into a continuous flow, and the distension of the tube which produces the recoil is caused by the *peripheral resistance.*

The whole mechanics of the circulation can be worked out on a model consisting of a syringe to represent the heart, elastic tubes to represent the bloodvessels, and a few clamps to offer the needful peripheral resistance. With such a model, if water be forced into the arterial tubes, the clamps being open and the peripheral resistance therefore very small, it is found, by means of a manometer, that the pressure in the arterial tube rises with each stroke of the syringe, and falls with the free pouring of the contents into the tubes representing the veins. As the peripheral resistance is small the pulsation set up in the fluid readily passes into the veins, and a manometer will here register nearly the same rise and fall as was met with in the arteries.

If, however, the vessels be clamped so as to produce a resistance, the first stroke of the pump causes the arteries to become distended, they then recoil, and while undergoing this they receive another stroke from the pump and become still more distended. Once more they recoil on their contents and are once more distended by the action of the pump, and so on. If all this time the arterial manometer be watched, it will be observed that the mercury or water rises with each stroke of the pump, but instead of falling at once to zero as it did in the unclamped tube, it only has time to fall a short distance before a second stroke of the pump sends it still higher than before; this is repeated at every stroke of the pump until the water or mercury refuses to rise any higher in the tube, contenting itself by rising to a certain height at each stroke of the pump, and falling to a certain level during the interval between one stroke and another. In other words, a mean pressure has been established in the tubes representing the arteries, which has been brought about by the *peripheral resistance*, the elastic recoil of the tube, and the pumping of the syringe. So long as these factors remain the same the mean pressure will not vary. If, however, the clamped vessels be released, so as to allow fluid to flow more easily into the tubes representing the veins, at once the manometer shows a fall in the mean pressure owing to the removal of a certain amount of resistance, and by removing this resistance completely the mean pressure falls to zero. The *mean pressure*, then, represents the force which is necessary to cause as much fluid to pass through the periphery as is being pumped into the system of tubes by the syringe; if the peripheral resistance is high the pressure is high, and *vice versâ*.

A careful study of this experiment places us in complete possession of the main facts of the circulation, but even up to this point we have not learned all the lessons it is capable of teaching.

If a manometer be placed on the venous side of the model, it will show a very low pressure at the time when the arterial pressure is high. If the arterial tubes be felt it will be observed that at each stroke of the pump they expand, producing what is known in living tubes as the *pulse*; this expansion of the tube is greatest nearest to the syringe, dying out entirely at the peripheral resistance. It is evident that if we loosen the clamps, and so reduce the resistance and lower the mean pressure, that pulsatile waves will pass over to the venous side of the model, and these can again be obliterated by screwing up the clamp. Lastly, our model if working at mean pressure will show the effect of injury to the arterial tubes; if these be pricked, a continuous jet of water shoots out, the strength of the jet varying with each stroke of the syringe, whilst an injury to the venous side produces no jet of water but only a trickling flow.

Practically this embraces our knowledge of the main facts of the circulation, for all we have found true of syringe, elastic tubes, and clamps, will be found true of heart, bloodvessels, and peripheral resistance. The heart has to keep the arteries full; the innumerable smaller arteries with their muscular coat supply the peripheral resistance. Under the influence of this and the contraction of the left ventricle the pressure in the arteries rises so high, and their distension is so great, that as much blood passes through the periphery during the contraction of the heart and the ensuing pause, as enters the aorta during the contraction of the left ventricle. The elastic system of arteries ensures that an intermittent is converted into a continuous flow and thus a perpetual pressure is kept up on the mass of blood during the heart's pause. By a contraction of the arterioles the peripheral resistance is increased and the blood pressure raised; by a relaxation of the arterioles the peripheral resistance is reduced and the blood pressure falls. We have stated that a contraction of the arterioles by increasing the resistance raises arterial pressure and as a rule lowers that in the veins. This holds equally true for the pressure conditions in the vessels of any locally circumscribed area of the body as for the vascular system generally. It must not, however, be forgotten that local effects may and do produce general effects. If, for instance, *one* artery alone contracts this must lead to an increase of arterial pressure, which produces an increased flow of blood through all the simultaneously uncontracted arteries on into the veins. When the contracted artery is small, so that the area it supplies is limited, the local effects are more marked than the general effects. If, on the other hand, the local area affected is at all large, the influence of changes in the arteries of this area on the general blood pressure may be very obvious. We shall meet with a striking instance of this when dealing with the action of the depressor nerve on blood pressure, through the medium of alterations in the arteries which supply the splanchnic area, by means of the splanchnic nerve.

Blood Pressure.—From what has been said, it is hardly necessary to define blood pressure as the pressure exercised upon the blood in the elastic vessels, resulting from the action of the heart and the peripheral resistance.

If the peripheral resistance is great through a contraction of the arterioles, the amount of fluid passing into the veins is reduced in quantity; a larger bulk of fluid will in consequence exist between the pump and its outlets, and the blood pressure rises. If, on the other hand, the blood is passing freely through the dilated arterioles the blood pressure falls. When the heart is more active, or when the arterioles contract, the blood pressure rises; when the heart is less active or the arterioles dilated the blood pressure falls. The mean pressure in the arteries is highest close to the aorta and lowest in the region of the periphery; the fall in pressure from the aorta to the periphery is gradual. At the minute arterioles the fall in pressure is sudden, and in the veins gradual and very slow; in fact, owing to causes to be dealt with in the chapter on Respiration, a negative pressure may exist in the great veins near the heart. Fig. 17 exhibits in a graphic form the fall in blood pressure in the different regions of the vascular system.

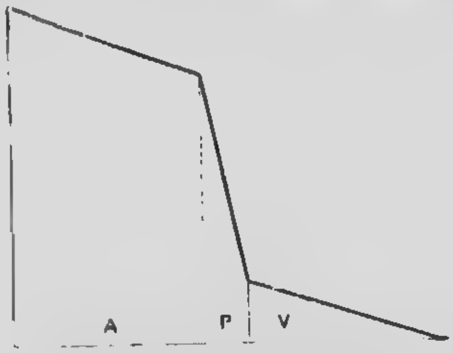


FIG. 17.—DIAGRAM OF BLOOD PRESSURE (FOSTER).

A, Arteries. P, Peripheral Region (minute arteries, capillaries, and veins). V, Veins. The ordinates represent the difference in blood pressure in the several regions of the vascular system.

In the carotid of the horse the pressure may be from 8½ inches to 12¾ inches of mercury (215 to 325 mm.), or equal to a column of blood from 9¼ feet to 13¼ feet in height; in the dog 4 inches to 6¾ inches of mercury (100 to 170 mm.), or 4½ feet to 7¼ feet of blood, and even in the rabbit a pressure of 3 feet of blood may be obtained. The first blood pressure experiment made was on a horse; the tube was placed in the femoral artery, and the blood rose 8 feet 3 inches in height.

In the following table is given, according to Volkmann, the mean pressure in the aorta of different animals:

Horse	12½ inches (321 mm.) to 6 inches (150 mm.).
Dog	6¾ inches (172 mm.) to 4¼ inches (104 mm.).
Sheep	8 inches (206 mm.) to 6¼ inches (156 mm.).

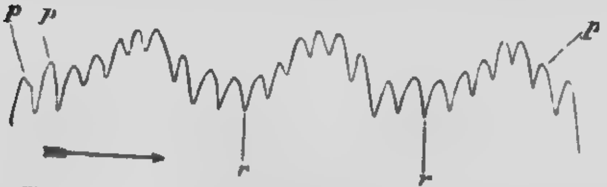


Fig. 18.—Tracing of Arterial Pressure with a Mercury Manometer (Foster).

The smaller curves *P*, *P* are the pulse curves due to the heart-beat. The space from *r* to *r* embraces a respiratory undulation. The tracing is taken from a dog, and the irregularities visible in it are those frequently met with in this animal.

The arterial pressure varies, as we have said, with each systole of the ventricle, but besides this there are also certain larger and longer undulations obtainable in graphic records of blood pressure, which are not due to the heart-beat but are caused by the respiratory movements (Fig. 18). Thus at every inspiration the blood pressure rises and at every expiration it falls. Speaking generally this is true, though the tracing (Fig. 19) shows that the pressure does not rise immediately inspiration commences, nor does it fall as soon as expiration begins. The cause of this will be explained when dealing with respiration.

The blood pressure in the capillaries is very difficult to ascertain. It is probably $\frac{1}{6}$ to $\frac{1}{7}$ of that in the large arteries or lies between 20 to 40 mm. of mercury.

Blood pressure in the veins is $\frac{1}{14}$ or $\frac{1}{15}$ of that in the large arteries. The greater the distance the veins are from the heart the greater the pressure, so that the highest pressure is in the peripheral veins and the lowest in the jugular. In a sheep the following values were obtained :

Jugular vein -	$\frac{1}{100}$ inch (0·2 mm.).
Facial vein -	$\frac{1}{8}$ inch (3 mm.).
Brachial vein - - -	$\frac{7}{16}$ inch (12 mm.).
Crural vein - - - -	$\frac{1}{2}$ inch (14 mm.).

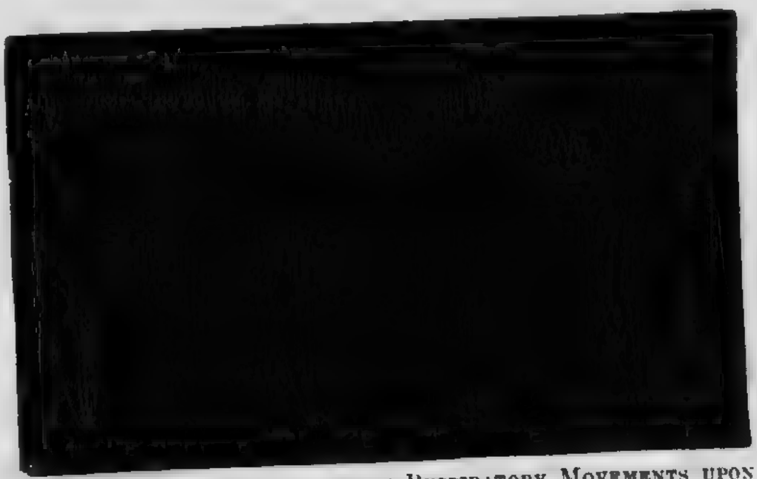


FIG. 19.—RABBIT. INFLUENCE OF RESPIRATORY MOVEMENTS UPON ARTERIAL BLOOD PRESSURE (WALLER).

The blood pressure is the upper tracing, the respiratory movement is the lower tracing. I is inspiration, E expiration.

In the large veins just as they enter the heart the pressure is very low, and here the manometer may show even a negative pressure at intervals ; in the anterior vena cava of the dog a negative pressure of $\frac{1}{8}$ inch of mercury (3 mm.) may be registered. This is due to inspiration, which by producing a negative pressure in the thorax assists the blood to reach the right auricle ; it is this negative pressure which in the human subject renders operations at the root of the neck dangerous, air being aspirated into the heart should the vessels be wounded. From observations on the horse the risk of air entering during operation may be neglected. Blowing air into the veins causes no discomfort until a considerable amount has been introduced. Even then only sighing respirations are produced.

The amount of blood which may be removed from the body without lowering the blood pressure is surprising. This is explained by the fact that the vessels adjust themselves to the reduced bulk of fluid in circulation; this adjustment is effected by means of a nervous apparatus to be dealt with presently, and in this way the blood pressure is kept up. Experiments show that it is not until two-fifths of the blood in the body have been removed that the blood pressure begins to fall; after cessation of hæmorrhage the pressure again rises, unless the loss of blood amounts to 3 per cent. of the body weight, in which case the low pressure becomes dangerously permanent.

It is astonishing how rapidly a deficiency in the circulating fluid is made good. The fact is that the tissues give up their fluid in an endeavour to replace the loss of blood, quite apart from the repair which is being effected through the thoracic duct. It is the loss of fluid by the tissues which causes the thirst of hæmorrhage.

Circulation in the Living Tissues.—The circulation in the living animal may be readily seen in the web of a frog's foot, or in the mesentery of a mammal, and in this way we learn exactly how the corpuscles behave within the vessels.

In all capillary vessels of small size the corpuscles pass through singly, sometimes revolving in the plasma, traversing certain sections very rapidly, others very slowly. In the vessels larger than the capillaries, such as the commencement of the small veins, the stream of blood behaves somewhat differently; in these the centre of the vessel is occupied by a column of red cells, whilst between them and the coats of the vessel is a clear layer or zone in which may be seen the white corpuscles strolling lazily along the sides, occasionally stopping, then moving forward once more. This difference in the behaviour of the corpuscles is due to the physical fact that the friction against the sides of the vessel is greater than in the centre; but apart from that, there appears to be an attraction exerted on the white corpuscles by the endothelium, so that they may, as previously pointed out, pass completely through the wall of the vessel into the surrounding tissue. This is especially well marked in inflammation, where the slowly moving white corpuscles become attached, as it were, to the lining of the vessel and collect in masses; with them also may be seen the blood platelets, which under the normal condition of circulation occupy the central zone of the vessel with the red blood cells. Under inflammatory action the white cells pass completely through the vessel wall in large numbers, aided, as previously pointed out, by their amœboid movements and the spaces existing between the endothelial plates of the vessel. This is known as the migration of white corpuscles. The essential changes taking place in inflammation occur in the wall of the vessel, and the passage of corpuscles through this is not limited solely to the white, but the red may also pass out. That inflammatory changes are essentially due to the condition of the vessel-wall and not to that of the blood, is proved by the fact that an artificial corpuscular fluid introduced into the inflamed part behaves exactly as does the blood.

The Pulse.—It is a fact of common observation that the arteries throb or pulsate whilst the veins do not, and we now have to inquire what really produces this pulsation, and why it stops at the arterioles.

When the left ventricle contracts and drives its blood into the aorta, the arteries distend to accommodate it and then recoil owing to their elasticity; each expansion of the arterial wall coincides with a contraction of the ventricle, and so each beat or throb of the pulse corresponds with a contraction of the heart. This intermittent expansion of the arteries gradually becomes less marked at a distance from the aorta, and dies out at the arterioles. We have previously (p. 58 and p. 61) drawn attention to the fact that the *elastic* properties of the arterial wall, together with the *peripheral resistance* in the smallest bloodvessels, convert the intermittent flow started by the heart into the continuous stream in the capillaries and veins. In seeking for the cause of the disappearance of the pulse we find it similarly in the elastic property of the arterial walls. In virtue of this property each inch of the arteries is engaged, by means of its sudden distension after each heart-beat and its more gradual elastic recoil before the next, in sheltering the capillaries from the effect of that beat. The oscillations of pressure which give rise to the pulse are, so to say, 'damped' by the elastic arterial walls, or in other words converted into a steady pressure, a fraction of the pulse being thus actually destroyed by each inch of the arteries. When all the fractions thus destroyed are added together we can readily understand why the initial 'jerk,' to which the pulse is due, has entirely disappeared just before it would otherwise have reached the capillaries. If the arterioles dilate considerably, when, in fact, less elastic recoil of their walls is called into play by the lessened peripheral resistance, it may be possible for the 'throb' to pass not only through the arterioles but also the capillaries, and appear in the veins; in this way a venous pulse may be produced. An example of this will be given when dealing with the influence of certain nerves on the vessels of the submaxillary gland of the dog, which cause dilatation of the arterioles and throbbing in the veins.

This intermittent expansion of the arteries, called the *pulse*, produces a wave in the arterial system which is spoken of as the pulse-wave. From what we have said it is evident that the height of this wave is greatest nearest the heart, and falls to zero at the capillaries. The wave travels with considerable velocity; from 15 to 30 feet per second. This may easily be determined by noting the interval between the commencing successive rises of two levers, resting consecutively on the wall of an artery, at a measured distance apart. The length of the pulse-wave is also considerable—viz., about 18 feet. This is arrived at by noting the time each single pulsation, travelling with the previously determined velocity, takes to pass completely under any *one* lever. Putting these data together it is evident that the beginning of each pulse-wave is lost in the arterioles before its end has left the aorta.

No mental confusion should exist as to the difference, and the causes of that difference, between the rate of transmission of the pulse-wave and the velocity of the onward flow of the blood. The factors which give rise to them are quite distinct. The pulse-wave runs along the surface of the blood-stream; the blood-current runs, as it were, within the pulse-wave; the former travels at a high speed, the latter comparatively slowly, at most some 15 inches per second. The case is similar to that of a wave seen moving rapidly over the surface of a slowly flowing stream.

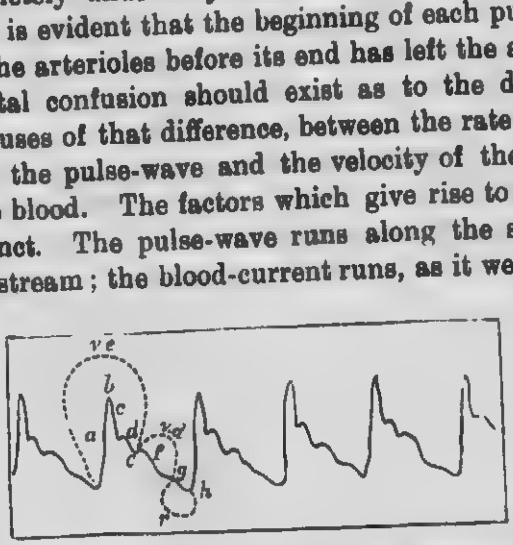


FIG. 20.—NORMAL SPHYGMOGRAM MODIFIED FROM DUDGEON; PRESSURE 2 OZ. (HAMILTON).

v.e, The period of ventricular systole; *v.d*, the period of ventricular diastole; *r*, the period of rest; *a*, *b*, *c*, primary or percussion wave; *d*, first tidal or predicrotic wave; *e*, aortic notch; *f*, dicrotic wave; *g*, second tidal wave.

The pulse-wave can be studied by means of the graphic method; it is obvious that a lever placed on a pulsating vessel will be moved up and down, and may be made to trace a curve which will record the passage of the pulse-wave under the lever at that particular spot. A tracing thus obtained, known as a *sphygmogram*, simply registers the expansion and recoil of the artery while the wave is passing; it will not give a tracing of the pulse-wave itself, which, as we have seen, is 18 feet in length. But we may at once say that unless the proper degree of pressure is kept on the vessel, great irregularity in the sphygmograms will be produced; it is held by some that certain of the tracings obtained are due to instrumental errors, and not to the true pulse-wave.

The simplest description of a sphygmogram (Fig. 20) is that it consists of a nearly vertical unbroken upstroke (the *anacrotic* limb), and an oblique downstroke (the *catacrotic* limb), which is broken by two or three waves known as *catacrotic waves*. Of these two or three waves *f* (Fig. 20) is one of the few which occurs with any regularity, and is known as the *dicrotic* wave. The notch *e* is described as the aortic notch, and is caused by the closure of the aortic valves.

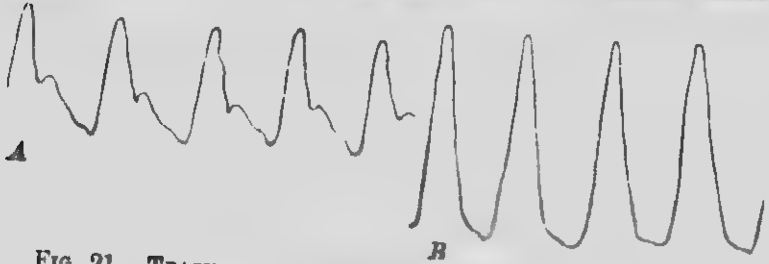


FIG. 21.—TRACING FROM THE FACIAL ARTERY OF THE HORSE (HAMILTON).

A before, *B* after destruction of the aortic valves.

The dicrotic wave is produced by a recoil of blood, the result of closure of the aortic valves; this reflected wave passes from the centre over the whole arterial system. The smaller waves in the catacrotic limb are either vibrations of the arterial wall, or reflections of the pulse-wave from the periphery towards the heart. That the dicrotic wave is a reflection from the aortic valves, is shown by the tracing in Fig. 21, taken from the facial artery of the horse, *A* before, and *B* after destruction of the valves. In *B* the dicrotic wave has disappeared. A well-marked dicrotic pulse gives a double beat of the pulse for each single contraction of the heart.

In connection with pulses the term **tension** has been employed by pathologists; thus pulses of high and of low tension have been described, and an attempt has been made to distinguish between the pathologist's tension and the physiologist's pressure. If tension be defined as the elastic force exerted by the artery on the blood within, it is evident that this bears some distinct relation to the force distending the artery, viz., the blood pressure; a high blood pressure and high arterial tension describe the same conditions. In an artery giving a high tension the dicrotic wave is nearly extinguished, the vessels in fact are so full that the recoil wave makes very little impression on the tense arterial wall; when blood pressure is low and the amount of movement in the artery great, the recoil or dicrotic wave is very marked (Fig. 22).

FIG. 22.—SPHYGMOGRAMS OF LOW TENSION, NORMAL, AND HIGH TENSION PULSES (WALLER).

The pulse varies in character, depending upon age, condition, and state of the system; it also differs according to the class of animal. The following table shows the pulse-rate in different animals:

Elephant - -	25 to 28	beats per minute.
Camel - -	28 ,, 32	,, ,,
Horse - -	36 ,, 40	,, ,,
Ox - -	45 ,, 50	,, ,,
Sheep - -	70 ,, 80	,, ,,
Pig -	70 ,, 80	,, ,,
Dog -	90 ,, 100	,, ,,

Certain variations occur in the pulse rate. It is always much quicker in the young animal than in the adult; the heart of a foal at birth beats 100 to 120 per minute, and that of a calf 90 to 130 per minute. As the animal increases in age the pulse rate drops, and in old age the pulsations are not only reduced in number but weaker.

The condition of the arterial wall alters the shape and nature of the pulse tracing in old age.

Between size of body and pulse rate there certainly appears to be some connection, and in the human family tall men have a slower pulse rate than short men of the same age.

The heart rate is rapidly responsive to all outside influence such as excitement or fear. A harsh word, fear, or timidity, will cause the pulse of a nervous animal to register nearly double the number of beats of the heart. To sickness or injury the pulse is instantly responsive, and is one of the cardinal aids both in diagnosis and prognosis. Variations of pulse rate follow as the result of work, so that a marked increase in the number of beats occurs; this means a larger amount of blood in circulation through tissues in a state of activity, and which consequently are in urgent need both of repair and flushing. In fact, there appears to be little doubt that it is the substance flushed out of the muscles during work which stimulates the heart either directly or reflexly, though other explanations have been offered, such as reflex stimulation of the sympathetics.

A relationship exists between heart rate and the condition of blood pressure; when the blood pressure becomes low, the heart rate increases as the result of reflex stimulation, by which means the output of blood is increased. If the temperature of the blood be raised the heart beat increases in frequency, and there appears but little doubt that one cause of the increased pulse rate in fevers is the actual temperature of the circulating blood. If the temperature of the blood be raised experimentally, it is found that a point is reached at which the heart ceases to beat; in the cat this has been found to be between 111° F. to 113° F. (44° to 45° C.).

The Velocity of the Blood varies in the arteries, capillaries, and veins, being greatest in the former, least in the capillaries, and rising again in the veins.

The velocity of flow is inversely as the sectional area of the tubes; the total sectional area of the capillaries is greater than that of the aorta, therefore the velocity is reduced; from the capillaries to the heart the area becomes smaller and the velocity increases. The velocity of blood-flow depends on the width of the bed formed by the vessels; as the arterial system expands, the velocity diminishes; in passing through the capillaries, with their immense network the velocity is at a minimum; in passing towards the heart the vessels are reduced in number, hence the bed is smaller and the velocity accordingly increased. The cause of the flow throughout the entire system is the contraction of the left ventricle, and the gradual fall in pressure which occurs from the aorta to the right auricle.

The vascular system has been compared to two cones placed base to base, the apex of one being the left ventricle, of the other the right auricle; where the bases of the two cones meet is the capillary network. The sectional area of this has been estimated by Volkmann as 500 times greater than that of the aorta, whilst the passage of blood through it is 500 times slower than in the aorta, owing to the width of the bed. According to the same authority, the velocity of blood in the carotid of the horse is from 11·8 inches to 15·75 inches per second (30 to 40 cm.); in the metatarsal artery of the horse 2·2 inches (5·5 cm.) per second, and in the jugular vein 8·85 inches (22 cm.) per second. A horse which gave a carotid velocity of 12 inches (30·5 cm.) per second gave a jugular velocity of 9 inches (22·75 cm.) per second. Chauveau found in the carotid artery of the horse a velocity of 20·47 inches (52 cm.) per second during systole, 8·66 inches (21·75 cm.) per second at the beginning of diastole, and 5·9 inches (15 cm.) per second during the pause.

The mean velocity in the carotid of the dog is 10½ inches (26·5 cm.) per second: at the end of diastole 8½ inches

(21·5 cm.) per second, and at the end of systole 12 inches (30·5 cm.) per second. The velocity of the blood is therefore increased by each systole of the ventricle, decreased during diastole, and falls still more during the pause. The flow in the arteries is assisted by expiration, while that in the veins is assisted by inspiration. The velocity of the blood is greater in the pulmonary than in the systemic capillaries, while in the venæ cavæ it is half of that in the aorta.

Any attempt made to estimate the velocity of the blood by dividing an artery, and measuring the escape of blood from its cut end in a given time, would lead to erroneous conclusions, for the velocity in a closed artery and an open one are two different things. In the undivided artery the peripheral resistance reduces the velocity, in the divided artery the peripheral resistance largely disappears and the velocity is five or ten times greater, so that the carotid of a horse does not bleed with a velocity of 16 inches per second but nearer 160 inches per second. Or to put it in a practical way, if the carotid of the horse has a sectional area of ·2 square inches, the amount of blood passing through the unwounded vessel amounts to 2 oz. per second, while if the same vessel be divided the loss of blood would be nearly 1 pint per second.

The **Duration of the Circulation** depends upon the length of time it takes a red corpuscle to travel from a given point and back to it again.* But there are many different paths it can take. For instance, from left heart through coronary vessels to right heart and again back to left heart would occupy a shorter time than a course through the liver, or through the feet or tail, so that a circulation time may mean nothing more than that a certain number of corpuscles have found the shortest cut through the circulation, or on the other hand have taken the longest. In a

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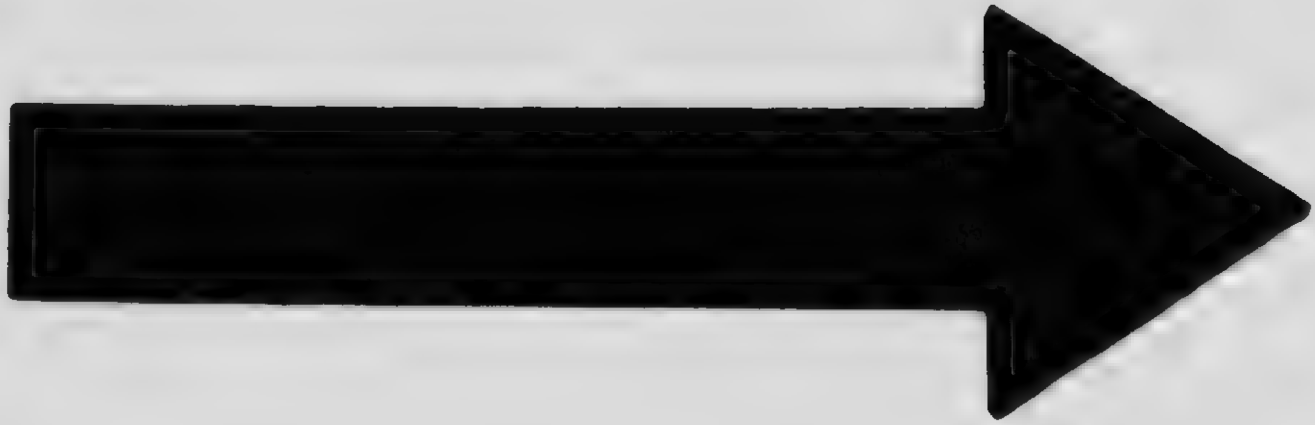
* The circulation time is determined either by injecting an easily distinguishable salt into the blood, or more precisely by increasing the electrical conductivity of the blood by injecting into it a neutral salt solution.



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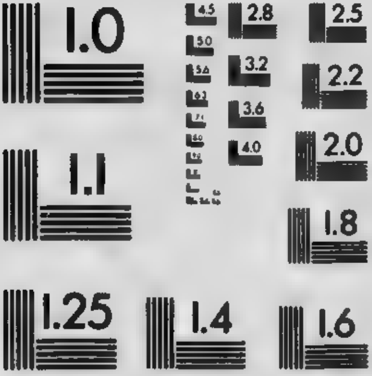

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horse with a pulse frequency of 42, the average complete circuit is performed in 31·3 seconds (Hering), and is equivalent, according to the latter observer, to about 28 beats of the heart. In the rabbit with a pulse frequency of 168 per minute, the time occupied in completing the round of the circulation was 7·79 seconds, or again in 28 heart beats; with the dog 16·7 seconds or in 26·7 heart beats.

Aids to the Circulation.—The contraction of the left ventricle is sufficient to drive the blood all over the body, but in the veins this force is assisted by the muscles compressing the vessels from without, while the presence of valves within prevents regurgitation. This is especially the case in the veins of the limbs where the fluid has to flow against gravity. The circulation in the large veins near the heart is assisted by the process of inspiration and the dilatation of the right auricle, both of which have an aspirating effect on the blood in the larger veins. The sucking action of the left auricle assists also in drawing the blood in the pulmonary veins towards the heart.

Influence of the Nervous System.—The bloodvessels are under the control of the nervous system acting on the muscular elements in their walls, by which means a reduction or increase in their size is produced. Such alterations are essential if a mean blood pressure is to be maintained; a rise in pressure in one part of the system may be compensated by a fall in another, and this is entirely brought about by an alteration in the diameter of the small arteries or arterioles. The evidence that the nervous system does possess this power over the bloodvessels, is furnished by the simple experiment of dividing the cord below the medulla, and maintaining life by artificial respiration. The immediate effect of division is an enormous fall in blood pressure; in the dog it will drop two-thirds below the normal, and this is due to the vessels dilating as the result of paralysis, their tone having been lost through the injury to the cord. From this experiment it is quite certain that structures above the section are responsible for the nerve control of the vessels, and these can be further localized by making a section above the medulla, the influence of which on the blood pressure is *nil*. It may, in fact, be readily shown that in the medulla, in the region of the fourth ventricle, is a small area the function of which is to produce and maintain the contracted condition of the bloodvessels defined as tone, and to this area the name *vaso-motor centre* has been given. By means of it the calibre of the bloodvessels throughout the body is regulated.

Experiment shows that in addition to the head centre, the medulla, there are subcentres for vaso-motor action in the cord. If, for example, the cord be divided in the lumbar region, the vessels of the hind limbs dilate, and the blood pressure falls; but if the animal be kept alive the blood pressure gradually returns to normal, the subcentre in the cord carrying out the work. This pressure is again at once lost by destroying the already divided cord.

Other, and perhaps more obvious, evidence of the influence of the nervous system over the bloodvessels is furnished by the ear of the rabbit, for if the sympathetic be divided in the neck, the ear on that side suddenly becomes flushed with blood, hot, and congested, and vessels not previously visible to the naked eye now become very apparent; and if the upper end of the nerve be stimulated, so as to imitate roughly the impulses passing along it in an intact condition, the vessels at once contract, the flushed appearance disappears, and the ear becomes cooler.

Since, in the above experiments, mere severance of the nerves which connect the bloodvessels with the central nervous system leads to a dilation of the arterioles, it is evident that impulses are, under normal conditions, being continually sent out along the nerves from the vaso-motor centres. These impulses keep the arterioles normally in a state of medium or partial constriction, and this condition is, as we have already said, known as arterial '*tone*.' Now, inasmuch as the function of the vaso-motor nerves is to regulate the blood-supply to any given area of the body in exact accordance with the varying needs of that area, 'tone' becomes a factor of the utmost importance in this regulative mechanism. Without it all the arteries of the body would, in the ordinary passive condition of rest, be dilated to their full extent; hence no increased supply of blood could be provided except by an augmented activity of the heart, which would, of course, affect the body as a whole, and not any one limited part of it. 'Tone' ensures that an arteriole may both dilate and contract, according as it receives less or more of the continuous constricting impulses, and thus the regulation of a varying blood-supply is made extremely perfect.

Hitherto we have only spoken of the constrictor influence over the bloodvessels, but the nervous system likewise exercises a *dilator* effect. In contrast to the constrictor influence, the dilator is not *tonic* in its action. It might be supposed that a dilator effect would naturally follow as the result of removing a constrictor influence from a vessel, without the intervention of a separate or antagonistic nerve supply; and this is exactly what does happen in most cases. But it is equally certain that special vaso-dilator nerves exist, of which perhaps the *chorda tympani* is the best example. This nerve supplies the bloodvessels of the submaxillary gland with dilator fibres; if the nerve be cut no evident change in the bloodvessels occurs, but if the end in connection with the gland be stimulated the vessels dilate, the arteries throb, and the blood passes through the gland with such rapidity that the venous blood becomes arterial in appearance. Much the same phenomenon occurs when the dilator nerves to the vessels of the penis are brought into activity. It is by no means certain that all vessels have both a constrictor and dilator nerve supply, in fact there are vessels in the body where no vaso-motor nerves of any kind can be demonstrated, such for example as the brain, heart, and lungs, while it is pretty certain that muscles do not contain any vaso-constrictor nerves.

It is here convenient to notice that the vaso-motor supply to muscles, which we have said is essentially dilator in effect, is brought into action reflexly when the muscle contracts. In this way an extra blood supply is furnished during the period of functional activity only.

No special centre has been demonstrated in connection with the vaso-dilator service, though several subcentres in the cord and medulla exist.

A consideration of the origin and distribution of the nerves governing the bloodvessels may now be undertaken.

The **vaso-constrictor** fibres for the whole body leave the spinal cord by the inferior roots from the first dorsal to the third or fourth lumbar. They do not at once pass to their destination, but through the medium of the white *rami communicantes* they enter the sympathetic nervous system, by linking up with the ganglia of that chain lying on either side of the spine. Up to the time of entering the ganglia the constrictor nerves are medullated, but after passing through it they lose their medulla, and a fresh lot of fibres, now non-medullated, arise and proceed to the bloodvessels.

The fibres for the *head and neck* are derived from the first four thoracic roots of the spinal cord, and having passed through the vertebral sympathetic ganglia they proceed to the inferior cervical ganglion, and by means of the cervical sympathetic pass to the superior cervical ganglion. From this ganglion fibres are sent out to supply the carotid artery and its branches.

The constrictors for *the fore limb* leave the cord by the fourth to the tenth thoracic roots, they pass into the stellate ganglion, from which, as grey rami, they emerge and join the cervical nerves which contribute to the brachial plexus, and through this supply the vessels of the fore limbs.

Those for the *hind limb* arise from the spinal roots from the eleventh dorsal to the third lumbar, and by white rami join the lumbar and sacral ganglia of the sympathetic chain; issuing from these as grey fibres, they pass into the sacral plexus, and supply all the vessels of the hind limbs.

The *abdominal* constrictor nerves are the splanchnics, greater and lesser, the former from the last seven dorsal, the latter from the first two or thee lumbar roots. The fibres pass to the semilunar ganglion of the solar plexus, and from this they issue as non-medullated fibres, supplying all the bloodvessels of the abdominal organs. The splanchnics are the chief constrictor nerves of the body; section causes a dilatation of the vessels they supply and a considerable fall in blood pressure, especially in those animals where the alimentary canal is largely developed as in herbivora.

It will be observed that the essential feature in the distribution of these constrictor nerves is that they pass through the sympathetic system before going to the bloodvessels; and from being medullated spinal nerves they become non-medullated sympathetic.

The **dilator nerves** in their distribution behave very differently to the constrictor; they leave the brain or cord by any cerebro-spinal nerve, they may or may not pass into a sympathetic ganglion before distribution, and in contrast to the constrictor fibres they pass direct to their destination, instead of taking a roundabout course; finally they do not lose their medulla until near their termination. Examples of typical dilator nerves have previously been given, viz., the chorda tympani to the submaxillary gland, and the nervi erigentes, stimulation of which causes erection of the penis; the former passes in company with a cranial nerve, and the latter with a spinal nerve to its destination.

Some spinal nerves contain both constrictor and dilator fibres, for example the brachial and sciatic nerves. On section of these the loss of constrictor influence is at first the most prominent feature, as shown by the hot flushed limb, but later, as the constrictor fibres degenerate, the dilator fibres become apparent, as on stimulation the constrictor nerves fail to react while the dilator nerves respond.

From what has been said, it is evident the nerve supply to the bloodvessels is elaborate and complex.

The vaso-motor centre both in the medulla and cord are extremely sensitive to the varying amounts of carbonic acid in the blood; an increased venous condition of blood leads to a constriction of the arterioles and a raising of the blood pressure. In asphyxia the arterioles remain constricted under the influence of the now intensely venous blood, as it stimulates the vaso-motor centre to unwonted activity, and though the initially high blood pressure subsequently falls to zero, it does not do so because the arterioles have relaxed, but because the heart has failed.

As previously mentioned, there is no single definitely located centre presiding over vaso-dilatation, though such may possibly exist.

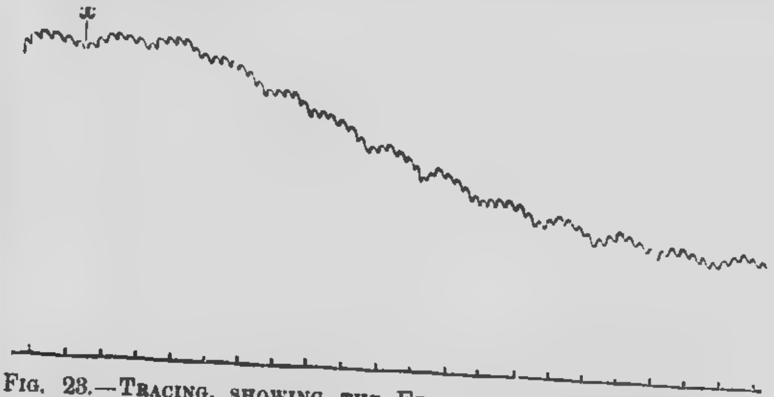

Fig. 23.—Tracing, showing the Effect on Blood Pressure of Stimulating the Central End of the Depressor Nerve in the Rabbit (Foster).

The time marker below marks seconds. At x an interrupted current is thrown into the nerve, and the blood pressure gradually falls.

The vaso-constrictor centre may be influenced reflexly by two distinct kinds of impulse, which pass from the periphery to the centre, the effect of which is either to stimulate or depress the centre; these are known as *pressor* and *depressor* effects, and the fibres which convey them are known as pressor and depressor nerves.

Pressor fibres are found in all sensory nerves, and stimulation of them produces an impulse which passes to the vaso-motor centre, from which constrictor impulses pass to the splanchnic area, causing contraction of the vessels and a rise in blood pressure.

The depressor nerve of the heart (see p. 50) is the best example of its class; by means of it impulses are conveyed to the medulla, and from there transmitted through the spinal cord and sympathetic system to the splanchnic area. The effect is to depress or lower the blood pressure by causing the abdominal arteries to dilate (Fig. 28)

Depressor fibres also exist which cause similar reflex vaso-dilator effects which are, however, too local to produce any general fall of arterial pressure, such as results from stimulation of the depressor nerve. Such a mechanism is in operation in erectile and other tissues.

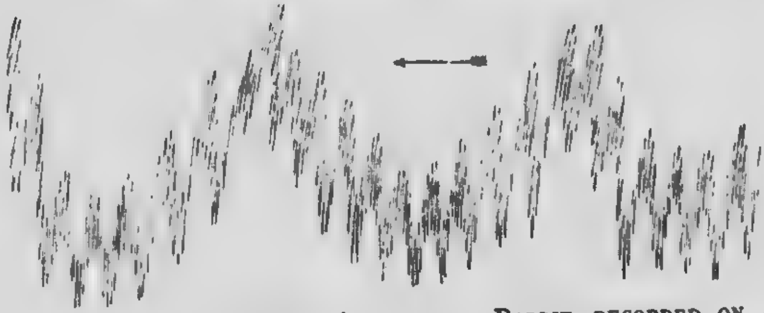

FIG. 24.—BLOOD PRESSURE CURVE OF A RABBIT, RECORDED ON A SLOWLY MOVING SURFACE, TO SHOW TRAUBE-HERING CURVES (FOSTER).

The heart-beats are the closely situated up and down strokes, readily seen by means of a lens. The next curves are those of respiration; the large bold undulations being Traube-Hering curves. In each Traube-Hering curve there are about nine respiratory curves, and in each respiratory curve about nine heart-beats.

Under certain conditions, such as asphyxia and hæmorrhage, the vaso-motor centre transmits to the vessels rhythmic constrictor impulses, which result in the appearance, on a simultaneous record of blood pressure, of undulations, known as Traube-Hering curves (Fig. 24). Such, of course, can only be detected by taking a tracing of the blood pressure. The existence of these waves is indicative of abnormal excitation of the vaso-motor centre.

When vessels are robbed of all nervous connections, they do not necessarily lose their powers of contraction; the muscular tissue of the arterial wall responds to the exciting influence of tension, so that increased blood pressure causes contraction and a reduced pressure relaxation of the vessel wall.

A very close parallelism exists between the nerve fibres which constrict the vessels and those which cause a more forcible contraction of the heart; in both cases they are of the non-medullated variety, in each they excite muscular action, and by so doing increase the wear and tear of the tissues involved. In the same way a close similarity exists between those fibres which dilate the bloodvessels and those which slow the heart; both are medullated and muscle-restraining, and in consequence both excite processes of repair rather than of disintegration.

Peculiarities in the circulation through various tissues occur as the result of their special function; they are observed in the brain, erectile tissues, etc. The great vascularity of the brain necessitates that the blood should pass to it with a degree of uniformity which will ensure the carrying out of its functions. We see this provided for in the frequent arterial anastomoses, for example, the Circle of Willis and the Rete Mirabile of ruminants, which ensures that not only does the blood enter with diminished velocity, but that if a temporary obstruction occurs in one vessel its work is readily performed by the others. The rete mirabile alluded to, which forms the arterial plexus on the base of the brain of ruminants, is considered by some to regulate the flow of blood to the brain when the head is depressed during grazing, and, it is said, accounts for the absence of cerebral hæmorrhage in these animals. It is probable that this may be one of its functions, but the horse possesses no rete, and his head is depressed during grazing for more hours out of the twenty-four than is the case with ruminants. It has probably, therefore, some other function to perform.

The pulsations observed in the exposed brain are not due to the pulse in the arteries, but arise from the respiratory movements; expiration causes the brain to rise by hinder-ing the return of blood, whilst inspiration causes it to fall by facilitating the flow.

The venous arrangement of the brain is very remarkable; the walls of the veins are composed of layers of the dura mater, and even portions of the cranial bones may enter into their formation. The veins or sinuses of the brain are large cavities, which from their arrangement are most unlikely to suffer from compression, and from the rigidity of their walls are not capable of bulging as most veins do when obstructed; in this way the easy return of the venous blood is provided for.

The cerebral circulation is considerably assisted by the presence of fluid within the ventricles of the brain. This fluid readily passes from ventricle to ventricle, and from ventricle to spinal cord; in this way, as the external pressure becomes greater the internal becomes less, and so compression of the brain substance is avoided. It will be remembered that no vaso-motor nerves have been satisfactorily demonstrated in the brain.

The singular arrangement of the venous plexuses of the corpus cavernosum penis, admits of this organ attaining a vast increase in size, a condition which in the brain every measure is adopted to prevent. The considerable size of the venous plexuses of the penis, their frequent intercommunication, the muscular pressure to which the veins leading from the sinuses are exposed, produce under the direction of the vaso-motor nervous system a considerable increase in the volume of the part.

In some other organs the distribution of the bloodvessels is also peculiar. It is not known why the spermatic artery and plexus of veins should take such a remarkably tortuous course; possibly, in some way or other, it may be concerned with the secretion of the glands, but its use is far from clear. On the other hand, tortuous vessels in the walls of hollow viscera, such as the stomach and intestines, perform a very evident function. We have only to think of the size of a collapsed and full stomach in the horse, to recognise the necessity for some arrangement existing to prevent stretching of the vessels or interference with the blood supply.

The vast venous and arterial plexuses of the foot of the horse are a peculiarity in the circulation dealt with in the chapter devoted to the Foot.

Pathological.

It is a remarkable fact that very little of the hard life of a horse falls on his arteries; with age the vessels become more rigid, but no sudden strain produces aneurisms, such as might be expected from the class of work performed. There is, however, one kind of strain which arises in the hunting field, or under similar circumstances, in which the walls of the external and internal iliac arteries suffer; in consequence of this a thrombus forms in the vessels, which become partly or completely obliterated. Collateral circulation suffices in a state of repose, during which not a sign of any circulatory trouble is evident, but as soon as the animal gets to work, sudden and painful muscular cramps occur, and finally temporary paralysis follows. These symptoms completely pass away with rest and return with work.

Parasitic trouble of the vessels is very common, the main seat being the anterior mesenteric artery, which is rendered rigid and aneurismal, and has its lumen obliterated by *Strongylus armatus*. It is remarkable how very little interference with the intestinal circulation occurs in consequence of this parasitic invasion, and it is equally astonishing how few horses are free from this infection. It is probably the most widely spread equine parasite.

Pulse.—The older physicians studied the pulse with care, at the present day it does not receive the same amount of attention. It is not sufficient to know the number of pulsations; the important point is the *character* of the wave.

A pulse may be *quick* or *slow*. Either of these may be *strong*, *weak*, *hard*, or *soft*. Strong and weak refer to the force of the ventricular contraction, hard and soft refer to the tension as judged by the finger—viz., the amount of pressure required to obliterate the pulsations. A further division of pulses is into *large* and *small*; this group refers to the volume of the artery. There is no pulse specially indicative of any given affection, but the *character* of the pulse in the prognosis of disease is of the utmost clinical value.

CHAPTER IV

RESPIRATION

Section 1.

The Lungs.

The lungs occupy the whole cavity of the thorax; during life no space exists between the pulmonary and costal pleura, so that the case is an air-tight one. So long as this air-tight condition is maintained, any movement which tends to increase the size of the case, such as the retreat of the diaphragm and the advance of the ribs, causes a distension of the sacs and the air rushes in; by a reversed process it is pressed out, viz., by a collapse of the chest wall. If, however, the cavity of the chest be opened to the external atmosphere the lungs collapse owing to their elastic recoil, and the fact that the atmospheric pressure within and without them is now the same. Such a condition would lead in the horse to asphyxia, as the pleural cavities communicate, but in those animals where the right and left pleural sacs are distinct, the lung on the wounded side only collapses.

The process by which the chest is filled with air, known as **Inspiration**, is a purely muscular act. The diaphragm as the chief muscle of inspiration contracts, and thereby recedes; the ribs are rotated, being drawn forwards and outwards, their posterior edges everted, and the intercostal space widened. By this means the capacity of the chest is increased and the lungs tend to fill the space thus created. By doing so they rarefy the air already within them, so that a difference in pressure occurs between the air in the lungs and that outside the body, and air rushes in to restore equilibrium; this inrush is inspiration.

The increase in the size of the chest which occurs during quiet inspiration in the horse is stated by Colin to be as follows: the antero-posterior or longitudinal diameter of the chest is lengthened between 4 and 5 inches (10 to 12·5 cm.), whilst the transverse diameter between the eleventh and twelfth ribs is increased by 1½ inches (4 cm.).

Only the last twelve or thirteen pairs of ribs, under ordinary circumstances, take any important share in respiration; this is due to the true ribs being more or less covered by the scapula and its attached muscles. When, however, a difficulty occurs in the breathing, the elbows are turned out which brings other muscles into play as auxiliaries in respiration, and a certain number of the true ribs now assist in increasing the capacity of the chest.

The **Movements of the Diaphragm** are interesting and peculiar; this large flat muscle with its thin tendon centrally placed works to and fro. In the body it is placed obliquely forwards, extending from the loins to the sternum, and the main to and fro movement occurs in its large upper half rather than in the narrower portion below. Through the centre of the diaphragm the posterior vena cava and œsophagus pass; it is obvious that any free movement of the diaphragm of this part would cause a 'pull' on these structures. This is prevented by movement occurring principally in the upper half and sides of the muscle, while the lower part and centre take very little share. When the diaphragm is receding, it carries back with it all the structures on the abdominal side which are adjacent to it; thus the liver, stomach, and spleen are especially affected by this movement.

The diaphragm is curved forward. This curve is produced by the pull exerted on the muscle by the air-tight thorax supplemented by the pressure from behind. The diaphragm never becomes flat, even under pathological conditions when the chest cavity contains gallons of fluid.

There is no flattening so long as the thorax is air-tight; as soon as air enters it would flatten if it were not for the abdominal viscera pressing it forward from behind.

In Fig. 25 is a diagrammatic horizontal section of the chest, looked at from above, showing the position of the diaphragm during inspiration and expiration and the displacement of the abdominal viscera. Observe the extent to which the sides of the diaphragm move as compared with the centre. The squeezing to which the liver is exposed must be an important help to its circulation, while the movements of the diaphragm must materially assist the flow of blood in the phrenic veins and posterior vena cava.

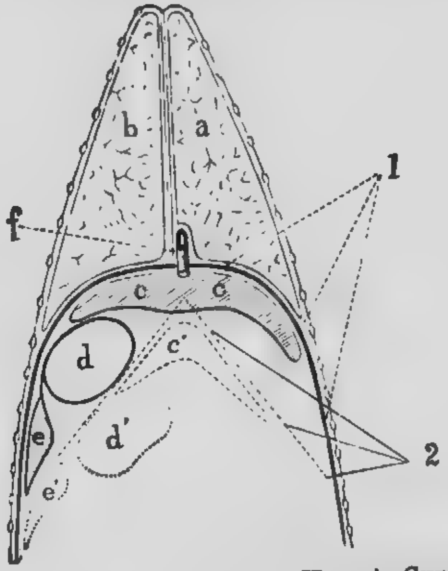

Fig. 25.—Horizontal Section of the Horse's Chest, looked at from above, illustrating the Movements of the Diaphragm (Sussdorf).

a, right lung; *b*, left lung. 1. Position of the diaphragm during deep expiration; *c*, liver during deep expiration; *d*, stomach during deep expiration; *e*, spleen during deep expiration. 2. Position of diaphragm during deep inspiration; *c'*, position of liver; *d'*, of stomach; *e'*, of spleen during deep inspiration; *f*, posterior vena cava as it passes through the diaphragm.

Fig. 26 gives a side view of the horse's chest, the diaphragm is attached around the margin AFE. The dotted line AE indicates the convexity of the muscle and the extent to which it bulges into the chest. The effect of this bulging is that the lungs rest on or wrap around the diaphragm, and, as it were, envelop it. The lungs do not reach as low as the cartilage of the false ribs, but about the breadth of a hand above them. The cut edges of the ribs in the above figure from F downwards indicate the lower and posterior margin of the lung; the sections of the ribs from A to C indicate the upper border of the lung. It is only the circumference of the diaphragm which is muscular,

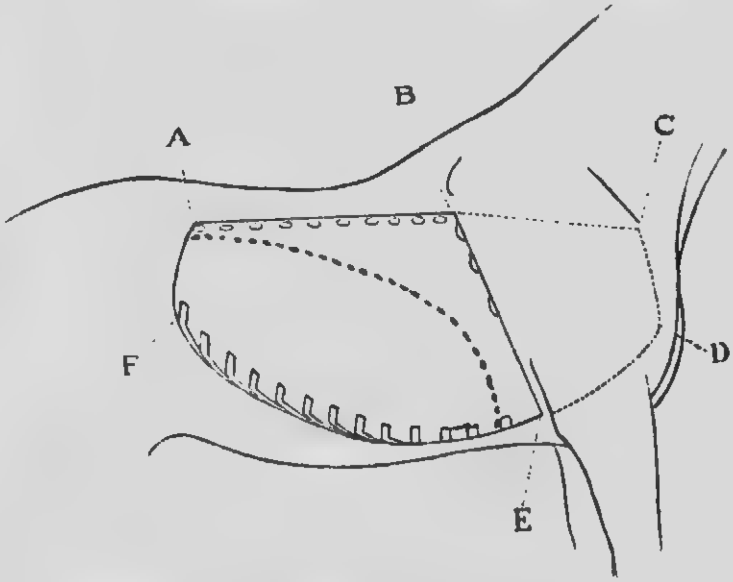

FIG. 26.—DIAGRAM OF THE EXTENT OF THE CHEST IN THE HORSE, AND POSITION OF THE DIAPHRAGM.

The area BCDE is under the scapula and its muscles, and practically not available for auscultation: the surface ABEF is the available area of the chest wall. The lung reaches to within a hand's-breadth of the false ribs. AF represents the last rib; BE runs parallel to the posterior edge of the triceps. CD corresponds to the position of the first rib.

The diaphragm bulges into the chest centrally, thus separating the two lungs; the curved dotted line falling from A to E represents the central line of the diaphragm, and shows the extent to which it encroaches on the chest.

and this muscular margin is widest at the sides and runs up to less than half the width above, where it is attached to the last ribs. The central portion of the diaphragm is a felt work of tendinous fibres, running from the muscle to the centre and in other directions. Filling in the upper and central portions of the diaphragm are large muscular pillars, attached to the spine, which support the considerable weight hung on the diaphragm, viz., the liver, with the stomach and contents. The diaphragm extends several inches behind its suspending pillars. Neither the muscle of the diaphragm nor the supporting pillars are markedly responsive to electrical stimulation as compared with voluntary muscle.

Expiration.—The chest having been filled with air, the next process is its expulsion, and the mechanism here concerned is not fully agreed upon by physiologists. Whilst some hold that it is a purely non-muscular act, others contend that certain muscles share in the process. All are agreed that the elastic recoil of the lungs is the important factor; there is also the elasticity of the cartilages of the ribs, which are seeking a return to their position of repose; and further, the elastic pressure of the displaced abdominal organs acting on the diaphragm; added to which is the contraction of the abdominal muscles, which presses the viscera still more firmly against the diaphragm. The factors named are sufficient in themselves to ensure that air is expelled from the lungs, though certain muscles attached to the ribs may facilitate their return to the position of repose.

The **Fœtal Lung** contains no air and therefore sinks in water. The first few inspiratory gasps at birth distend the alveoli, but for some time the conditions present in the adult, viz., the negative pressure in the pleural cavity, and the collapse of the lungs on opening the chest, are not found in the very young animal. Such only occur when the cavity of the thorax is larger than the lung in a state of collapse. In the fœtus the lungs exactly fill the chest in the condition of expiration, and it is not until the chest cavity grows, as it were, too large for the lungs that a negative pressure in the thorax is produced. Later on (p. 112) the cause of the first act of breathing will be explained. Thoracic development in young animals is very rapid; a foal will increase 1½ inches (4 cm.) in circumference within the first few hours after birth; when this absolute increase in chest capacity is established, a negative pressure in the pleural cavity is obtained.

Muscles of Respiration.—The action of the muscles of the chest during respiration has been much disputed. The external intercostals doubtless, from the direction taken by their fibres, pull the ribs forward, and by so doing increase the transverse diameter of the chest; in this respect they are regarded as inspiratory muscles. The internal intercostals, the fibres of which run in an opposite direction to the external, draw the ribs backwards and act as muscles of expiration; and speaking generally, we may say that those muscles which draw the ribs forward are inspiratory, whilst those which draw them back are expiratory. The following table shows the inspiratory and expiratory muscles of the chest:

Muscles of Inspiration.	*Muscles of Expiration.*
Diaphragm.	Abdominal muscles.
External intercostals.	Internal intercostals.
Serratus anticus.	Transversalis costarum.
Levatores costarum.	Serratus posticus.
Serratus magnus (during difficult respiration).	Triangularis sterni
Latissimus dorsi " "	
Scaleni " "	

In some animals the ribs do very little work and the diaphragm becomes the chief respiratory muscle. In most quadrupeds the sternum is fixed to the ribs and undergoes little or no movement; even the most powerful respiratory movements in the horse give rise to no sternal movement. On the other hand, there is a moderate amount of movement between the sternal ribs and the cartilages. During laboured respiration any muscle which can assist in advancing the ribs directly or indirectly is brought into play. This is well marked in dyspnœa.

After the expiratory act there is a pause before the next inspiration. In the horse at rest the period of expiration is as a rule longer than that of inspiration, though the proportion between the two is not invariable. During work the value of the inspiratory and expiratory acts is about equal.

During inspiration a slight **negative pressure** exists in the trachea, and during expiration a slight positive pressure. In the pleural cavity a negative pressure is always present, due to the tendency of the elastic lungs to collapse. The value of this pull of the lungs on the chest wall has been ascertained for the sheep to be about ⅛ inch (3 mm.) of mercury, and during dyspnœa ⅜ inch. In the dog during inspiration the negative pressure in the pleural sac is ¼ inch (6 mm.) of mercury, whilst during expiration ⅛ inch (3 mm.) has been observed. In the horse ¼ inch (6 mm.) has been registered during a powerful expiration, and 1⅛ inches (28 mm.) during a powerful inspiration. The negative pressure can be recognised post-mortem by the rush of air immediately the chest is punctured.

The **number of respirations** varies with the class of animal; as a rule, the larger the animal the slower the respirations:

Horse	8	to	10	per	minute.
Ox	12	„	15	„	„
Sheep and Goat	12	„	20	„	„
Dog	15	„	20	„	„
Pig	10	„	15	„	„

Rumination increases the frequency of respiration, and muscular exertion in all animals at once causes it to rise. In experiments on respiration this is most marked; walking a horse will nearly treble the number of respirations, but the breathing begins to fall immediately the horse stops, though it does not reach the normal for a few minutes.

The ratio of heart-beats to respiration has been placed at 1 : 4 or 1 : 5.

The Effect of Respiration on Circulation.—We have previously alluded to the influence of respiration on the circulation, and the assistance this renders in aspirating the blood into both sides of the heart; further we have drawn attention to the value of the negative pressure in the chest in connection with the diastole of the heart.

The whole of the negative pressure found in the heart (p. 87) is not due to the diastole alone, but to the diastole plus the aspiratory movement, for if the chest be opened a smaller amount of negative intra-cardiac pressure is registered.

In dealing with blood pressure (p. 63) attention was drawn to certain undulations of respiratory origin. These are produced by the decrease of pressure on the vessels of the thorax during inspiration; this reduction of pressure is small, but it produces sufficient suction to affect sensibly the thin-walled veins opening into the right auricle, the blood pressure in which is very low. By this suction more blood is aspirated at every inspiration into the right auricle, and consequently more blood is ejected from the left ventricle. In this way we have the arterial pressure raised during inspiration, followed by a fall during expiration (see Fig. 18, p. 63). But the rise does not take place immediately inspiration begins, nor does the fall occur immediately expiration starts, but shortly after in both cases, as may be seen in Fig. 19, p. 64. The explanation of this is that the pulmonary vessels have a greater capacity during inspiration than during expiration, and the increased amount of blood entering the right heart on inspiration is first used to fill the pulmonary vessels, and this accomplished, the general blood pressure rises by the excess being passed on to the left heart; similarly the fall does not occur immediately expiration begins, as the pulmonary vessels have not yet returned to their expiratory capacity.

In examining the blood pressure and respiratory curves of the dog, it is observed that the pulse frequency is increased during inspiration, and reduced during expiration; this reduction in the frequency of the pulse is due to the stimulation of the cardio-inhibitory centre, whilst the increase is caused by a diminished activity of the inhibitory mechanism (see p. 48).

In speaking of inspiration raising blood pressure we must not forget the mechanical advantages of a contraction of the diaphragm compressing the liver and posterior vena cava, and so forcing more blood towards the heart; this no doubt is another cause of the rise of blood pressure during inspiration.

The Nostrils.—Before the air reaches the lungs it is warmed by passing through the nasal cavities, so that it enters the trachea at nearly the body temperature. The incoming air also becomes saturated with watery vapour; this saturation likewise occurs in the nasal chambers. In the majority of animals air may pass either through the nose or mouth to enter the trachea, but in the horse, owing to the length of the soft palate, nasal respiration alone is possible; we therefore find in this animal the nasal chambers with their inlets and outlets well developed. The opening into the nostrils of the horse is large, funnel-shaped, and capable of considerable dilatation; it is partly cartilaginous, and partly muscular. Immediately inside the nostril is a large blind sac, termed the **false nostril**, and one of its uses appears to be to increase the capacity of the nasal opening by allowing considerable and rapid dilatation. Another use is in the production of the peculiar snorting sound made by a horse either when he is alarmed or very 'fresh.'

During forced inspiration the nostril expands, especially the outer segment, viz., that part in communication with the false nostril, and the air is rapidly drawn up through the nasal chambers; during expiration the outer segment of the nostril collapses, but the inner segment, composed principally of the cartilaginous ala, dilates. Thus the movement of the outer and upper part of the nostril is principally inspiratory, of the lower and inner part mainly expiratory, producing a peculiar double motion of the nostrils well seen after a gallop or in acute pneumonia (Fig. 27). The dilatation of the inner segment of the nostril is brought about by muscular contraction and by the rush of expired air; striking the cartilaginous wing of the nostril the current is directed outwards at an obtuse angle to its course down the nostrils, as may be well seen on a frosty morning when a horse is respiring rapidly.

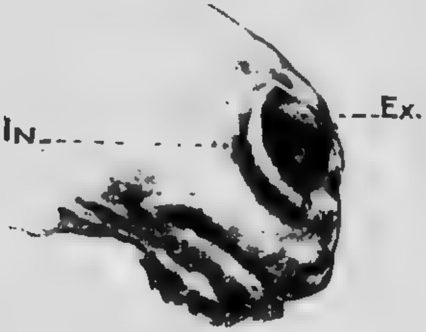

Fig. 27.—Nostril of Horse.
In, The inspiratory portion; *Ex*, the expiratory portion.

The nasal chambers are remarkable for their great depth and narrowness; the cavities are partly filled by the turbinated bones, which nearly touch the septum on each side, so that a deep but thin column of air passes through the chambers; the result of this arrangement ensures that the air is saturated with vapour and raised to the proper temperature.

The nasal chamber is divided into two parts, the lower or respiratory and the upper or olfactory. The latter will be dealt with under the Senses. It comprises the upper portion of the superior turbinated bone, ethmoid cells, and a portion of the middle meatus; the respiratory channel on the other hand lies on the inferior part of the nasal chamber and comprises the inferior meatus, inferior turbinated bone, part of the superior and part of the middle meatus.

The Glottis.—The air having been warmed by passing over the septum and turbinated bones, enters the glottis, the arytenoid cartilages being separated to a greater or less extent to enlarge the opening. In quiet respiration this enlargement of the glottis is not very marked, but during work the cartilages are powerfully drawn upwards and backwards, and the V-shaped glottis fully opened (Figs. 32 and 33, p. 124). It is a remarkable fact that the laryngeal opening should be so relatively small, considering the diameter of the trachea and the size of the nasal openings.

During inspiration the larynx and trachea slightly descend, while they ascend during expiration. This is particularly well seen in horses during the hurried respirations of disease, producing a well-marked rhythmical movement of the laryngeal region and base of the tongue.

The Facial Sinuses are cavities in the face communicating with the nasal chambers; they are of considerable size, occupy nearly the entire facial region, and they give the needful bulk to the head without adding to its weight; they are lined by a membrane which is continuous with that of the nose. These sinuses are filled with air which enters them through a foramen at the posterior part of the middle meatus; during every act of respiration air is passing in or out of them. At first sight it would appear that air ought to enter the sinuses during inspiration, but the reverse is the case; it is only during expiration that they are filled, whilst during inspiration air is sucked out. Considering the position of the common inlet to these sinuses, it is difficult to understand why they should fill during expiration, though the advantage of hot instead of cold air entering is evident.

Respiratory Changes in the Air and Blood.—The changes which the air undergoes on passing into the lungs must now be considered.

ATMOSPHERIC AIR CONTAINS IN 100 PARTS:

	By Volume.	*By Weight.*
Oxygen	20·96	23·015
Nitrogen	79·01	76·985
Carbonic Acid	·03	—

The above gases are the essential constituents of the atmosphere; the new elements argon and krypton have, so far as is known, no physiological significance, and in the table are included in the nitrogen.

The proportion of carbonic acid is small; it is a natural impurity in the air, though essential to plant life. The atmosphere also contains moisture the amount of which depends upon the temperature; the higher the temperature the greater the amount of water which the air can contain as vapour, and the lower the temperature the less the amount. Air may be dry or saturated, the latter term implying that it contains as much vapour as it can hold at the observed temperature; it generally contains about one per cent. of moisture, and is spoken of as dry if it contains one-quarter per cent. The air which passes from the lungs is always saturated with moisture.

When air is taken into the lungs it alters in composition: it loses a proportion of its oxygen and gains in carbonic acid, as may be seen in the following table:

	Nitrogen.	*Oxygen.*	*Carbonic Acid.*
Composition of inspired air	79·01	20·96	0·03
” expired air	79·01	16·02	4·38
		−4·94	+4·36

The volume of oxygen absorbed is slightly greater than that of the carbonic acid which takes its place, so that if dried and reduced to standard barometric pressure and temperature, the volume of *dry* air expired is slightly less than that of the air inspired. But since expired air is usually warmer than inspired (not always in the Tropics) and is saturated with aqueous vapour, the volume expired is actually greater.

The proportion which the volume of oxygen absorbed bears to the volume of carbonic acid given off is termed the respiratory quotient, and is expressed as $\frac{CO_2}{O_2}$. The quotient varies with different animals, and depends upon the nature of the diet. On a carbo-hydrate diet less oxygen is required, for the reason that the oxygen and hydrogen in the molecule exist in the proportion to form water, so that oxygen is required for the carbon only. On a fat diet oxygen is required for both the hydrogen and carbon in the molecule.

In herbivora	the respiratory	quotient is	·9	to 1·0
In carnivora	,,	,,	·75	,, ·8
In omnivora	,,	,,	·87	

That is to say, for every 1 part of oxygen absorbed by herbivora there is produced ·9 to 1 part of carbonic acid, and for every 1 part of oxygen absorbed by carnivora ·75 to ·8 part of CO_2 is produced. In carnivora it will be observed that the amount of CO_2 produced is considerably less than the amount of oxygen absorbed, for the reason that the latter instead of being devoted to the oxidation of carbon and reappearing as CO_2, is employed in the oxidation of hydrogen and returned as water. The value of the respiratory quotient lies in its being a measure of the combustions occurring in the body as a whole; as a rule the amount of carbon dioxide formed is less than the oxygen absorbed, but there are exceptions, and a respiratory quotient may be above unity as in hibernating animals in storing up fat for the winter, and it is not unknown among other animals after a diet rich in carbo-hydrates. In such cases the CO_2 discharged is in excess of the oxygen absorbed, the necessary oxygen contained in the CO_2 being obtained from the intra-molecular store, of which we shall hear presently. These high quotients are only observed where the conversion of carbo-hydrates into fats is occurring, as in the fattening of animals.

There are other gases returned from the lungs besides carbonic acid and oxygen, but very little is known about them. According to Reiset, both **hydrogen** and **marsh gas** are given off in the expired air of ruminants, in fact, he places the latter at 188 cubic inches in 24 hours. Both are supposed to be derived from the intestinal canal, being absorbed into the blood by the vessels of the intestinal wall. In our observations on the gases of respiration of horses, it was found after deducting the oxygen, carbonic acid, and nitrogen, that a balance remained the nature of which was unfortunately not ascertained; possibly it was a mixture of hydrogen and marsh gas, but it did not amount to anything like the quantity found by Reiset.

The nitrogen of the air is returned unaltered.

We have previously learnt the changes occurring in the blood during its passage through the lungs; we have now to study the way in which the interchange of gases between this fluid and the air is brought about.

Absorption of Gases in Liquids.—The law regulating the absorption of gases by fluids is very clear. Every fluid in which a gas is soluble absorbs the same *volume* of gas, no matter what the pressure may be; but as the number of molecules in a gas depends upon the pressure, it is evident that the *weight* of the absorbed gas rises and falls in proportion to the pressure; this is known as the law of Dalton and Henry.

The volume of gas absorbed by a fluid depends upon the nature of the gas; for instance, 1 volume of water will absorb 1180 volumes of ammonia gas, whilst the same volume of water will only absorb ·00193 volume of hydrogen. The temperature of the water is also an important factor, for the higher the temperature the less the gas absorbed.

If, now, instead of taking a single gas to be absorbed by a fluid we take a mixture of gases, it is found that the volume of each gas forming the mixture is absorbed as perfectly as if it were the only gas present; no more and no less is absorbed, whether the gas be by itself or whether it form only a proportion of the mixed gases present.

This is explained as resulting from the fact that one gas does not exercise any pressure upon the other gases with which it forms a mixture. The term used by Bunsen to define the pressure exerted by one gas in a mixture of gases is '*partial pressure.*' For example, 100 volumes of air contain at freezing-point and standard barometric pressure (30 inches) 21 volumes of oxygen and 79 volumes of nitrogen; what is the partial pressure exercised by each gas in this mixture?

$$\frac{30 \times 21}{100} = 6\cdot3$$ inches of mercury, which is the partial pressure of the oxygen;

and

$$\frac{30 \times 79}{100} = 23\cdot7$$ inches of mercury, which is the partial pressure of the nitrogen.

The term 'partial pressure' occurs so constantly in the following pages, that the above may help to make the matter clear.

If a mixture of gases, say the atmosphere, be exposed over a fluid already containing some of these gases dissolved in it, it is found that if the proportion of dissolved gases in the fluid is less than their proportion in the atmosphere, the latter pass into the fluid until the amounts of gases in the fluid and that in the air are equal. On the other hand, if the fluid contains more dissolved gas than the atmosphere above it, gas will pass from the fluid to the atmosphere until the amounts in each are equal. This is really a process of diffusion, and plays a most important physical part in respiration; it is one of the means by which the carbonic acid passes from the blood into the air-cells, and the oxygen from the air-cells into the blood.

If two different gases be placed in a jar, in a short time a complete mixture will have occurred, as both gases pass each into the other until a thorough and equal mixture has taken place. This is termed the process of *diffusion*, and is the chief means by which the air in the deeper part of the lungs mixes with the fresh air introduced by breathing.

Such are the physical laws which it is necessary to understand before the processes involved in respiration can be fully comprehended.

The Respiratory Exchange in the Lungs and Tissues.—The respiratory exchange in animals is of two kinds: the *external respiration*, which takes place between the air and the blood through the medium of the lungs, and the *internal respiration*, which occurs between the tissues on the one hand and the blood and lymph on the other. As we shall see, both are complex questions which are far from settled.

The blood having been robbed of about 35 per cent. or more of its oxygen in the tissues, the hæmoglobin makes its way back to the lungs in a partly reduced condition; here it circulates through the vast capillary system spread over the alveoli of these organs, and is brought as closely as possible into contact with the air (alveolar) in the ultimate air-passages. Between it and the air we have only the membrane of the air-sac and the wall of the capillary, both of which are bathed in fluid; through this wet membrane the oxygen instantaneously passes, being greedily absorbed by the hæmoglobin of the red cells; of necessity the gas must first pass into the blood plasma, and from there it is taken up by the red corpuscles. The oxygen is not simply absorbed by the red cells, but forms with the hæmoglobin a weak chemical compound. Experiment has clearly shown that the union of hæmoglobin with oxygen is largely independent of pressure, and therefore does not obey the law of Dalton and Henry, which it certainly would do if simply absorbed.

We have yet to learn how it is that the oxygen in the air-vesicles passes into the capillaries to form this chemical union with hæmoglobin. Here we have one of the physical laws brought into play which we have previously described. When the venous blood arrives in the lungs it has lost much of its oxygen, the partial pressure of the oxygen is low, whereas the partial pressure of the oxygen in the atmosphere of the air-cells is relatively high; the result of this is that practically instantaneous diffusion occurs through the moist membrane separating the gas and the fluid. The oxygen entering the blood plasma unites at once with hæmoglobin; the latter takes up all or nearly all the oxygen it is capable of holding (an amount which is much greater than if simple absorption of oxygen by hæmoglobin occurred), and distributes it to the tissues through the medium of the arterial circulation.

The tissues are greedy for oxygen; their oxygen pressure is practically *nil;* once more diffusion occurs. The high partial pressure of the oxygen in the arterial blood becomes (through loss of oxygen to the tissues) low partial pressure in venous blood, and the partly reduced hæmoglobin is carried to the lungs, where the process just described is repeated. But the loss of oxygen to the tissues is not the only change the blood undergoes, for not only is its hæmoglobin partly reduced, but as the outcome of tissue activity increased quantities of another gas are added to it. The gas alluded to is carbonic acid; this is largely taken up by the venous blood and conveyed to the lungs, and the method by which it is got rid of will be explained presently.

The **fate of the oxygen** in the tissues is quite unknown. It is supposed to be stored up in some way or other until required, but in connection with this subject it is necessary that we should glance at *internal respiration*—viz., the respiration which takes place in the tissues.

The most remarkable feature in the respiration of muscle (and we select this tissue to elucidate the point under consideration) is that although the working of a muscle cannot occur without oxidation processes taking place, yet no free oxygen can be obtained from it; the partial pressure of oxygen in muscle is practically *nil.* Yet oxidation processes are occurring in muscle, and under such conditions that no free oxygen can reach it, as, for example, when the muscle preparation of a frog is placed in an atmosphere of hydrogen. Such a muscle preparation may be made to contract in an atmosphere of hydrogen and produce carbonic acid, without there being a trace of free oxygen either in the atmosphere surrounding it, or in the muscle itself, and this process may be continued until the muscle is exhausted.

The question is, therefore, How does the oxygen-free muscle obtain oxygen for the production of CO_2? In other words, what becomes of the oxygen taken to muscles? Few things in the whole range of physiology are more difficult to understand: oxygen goes to the muscle, it uses oxygen, yet no free oxygen is found in it!

It is supposed that when the oxygen reaches the muscle it is stored up in its substance amongst the muscle molecules, hence it has been termed intra-molecular oxygen; it there forms a complex substance which readily yields carbonic acid and other matters on decomposition, and this passes into the bloodvessels of the muscle and is carried away to be got rid of at the lungs.

It has been suggested that the storing up of oxygen in the tissues may be closely allied to the storing up of oxygen by hæmoglobin, though with this difference, that the compound which holds the oxygen in the tissues is more stable than the oxygen-holding substance in the blood. All we know of the fate of the oxygen is that it eventually determines the production of certain changes in the tissues, which lead to the formation of carbonic acid and other substances; but the changes which the oxygen undergoes from the time it leaves the blood and passes into the muscle substance, to the moment it issues from the tissues united with carbon as carbonic acid, are completely unknown.

The oxidations taking place in muscle and in every other tissue in the body occur in the substance of the tissue and not in the blood or lymph surrounding it. Experiments made to determine whether oxidations occur in the blood have failed, although readily oxidizable substances have been employed for the purpose. We have said the tissues are greedy for oxygen and use it up or store it away as quickly as it arrives; here is a very good example of their action in this respect. If a comparatively stable oxygen-holding substance such as methylene blue be injected into the circulation and the animal destroyed, it is found that although the blood is dark blue in colour, yet the tissues are normal in appearance until they are exposed to the air, when they turn a vivid blue. The explanation is that the tissues have robbed the methylene blue of oxygen and formed a colourless reduction product, which on exposure to the air takes up oxygen and again forms methylene blue.

Fate of the Carbonic Acid.—In the systemic capillaries the partial pressure of the carbonic acid is lower than the partial pressure of this gas in the tissues, the result of which is that it is hurried into the blood by the process of diffusion; but here, as with oxygen, simple absorption of the gas by the plasma would not be sufficient for the purpose of carrying off the whole of the CO_2 resulting from tissue activity, so that there must be some substance in the blood capable of fixing CO_2 until the lungs are reached.

If the serum of blood be exposed to the vacuum of an air-pump, it is found to yield little oxygen but a quantity of CO_2; it yields little oxygen because, as we have already learned, this is combined in the red cells; but the fact that it yields large quantities of CO_2 points to the blood plasma as the chief means by which this substance is carried. It has been determined experimentally that blood plasma will absorb more CO_2 than the same quantity of water, and it is evident, therefore, that there is something in the plasma which assists in carrying it. What this 'something' may be is doubtful, but it is generally believed that the sodium carbonate of the blood unites with a portion of the carbonic acid, though other substances may assist. Between the amount absorbed by the plasma, and that held in chemical combination by certain salts of the plasma, the total amount is carried along in the venous blood-stream, the partial pressure of the CO_2 in this fluid being high. On arriving at the lungs the venous blood circulates through the capillary network spread over the walls of the alveoli, the same wet membrane intervening between it and the external air as was described in speaking of the oxygen. The partial pressure of the CO_2 in the air of the air-sacs being lower than that of the blood, diffusion occurs between the blood and the air, the CO_2 passing out until equilibrium is established. The air now in the alveoli of the lungs having lost some of its oxygen, and considerably gained in its carbonic acid—in other words, having the partial pressure of its gases altered—diffusion between the air in the ultimate air-cells and bronchial tubes rapidly occurs until the balance is restored, thus rendering the air in the alveoli fit for further blood-reviving processes.

We have dealt with the CO_2 in the blood as if it were entirely carried by the sodium carbonate, but doubt is cast on this view, and Bohr states that CO_2 and hæmoglobin form a loose chemical compound, the CO_2 uniting with the proteid portion of the molecule, thus leaving unaffected the iron moiety with which the oxygen is united. The carbon dioxide hæmoglobin in this way carries one-third of the CO_2 from the tissues to the lungs, and under the influence of the oxygen in the air of the alveoli the CO_2 is expelled from the corpuscles and discharged into the alveoli. The manner in which the combined oxygen is liberated in the tissues, and the combined CO_2 liberated in the lungs, is explained by saying that certain gases have a tendency to leave the substances with which they are united, when the pressure in the surrounding medium becomes reduced; this process is termed 'dissociation.' Dissociation liberates the oxygen in the tissues where the oxygen pressure is *nil*, and assists in liberating the CO_2 in the lungs, where the CO_2 pressure is low, from the substances with which these are chemically combined, viz., hæmoglobin and sodium carbonate.

In treating of the exchange of gases between the alveolar air and the blood, diffusion has been represented as the only factor at work; but it is urged by some physiologists, that the cells lining the vessels and alveolar walls cannot be mere passive witnesses of these remarkable changes, but like the cells in other parts of the body are capable of taking an active share in local matters. In other words, there is a vital aspect to this question, as well as a physical and chemical one. An experiment of Haldane's with carbon monoxide is very suggestive in this respect. He found that though he could, outside the body, get 31 per cent. of hæmoglobin to combine with the gas, yet when air, containing the same percentage of CO as that to which the hæmoglobin had been exposed, was inhaled for even three or four hours, no more than 26 per cent. of the hæmoglobin of the blood combined with it. In other words, the cells of the pulmonary alveoli would appear to possess that same selective power which may be seen elsewhere, as, for example, in the kidney, and preferred to allow oxygen rather than carbon monoxide to pass.*

The respiratory exchange is influenced by age, being more energetic in young than in adult animals; this may be due not only to actually increased metabolism, but also to size. It is a well-known fact that the metabolism in a mouse is relatively much greater than in a horse; it is a question of weight and surface. The larger an animal the smaller the proportion between its weight and the extent of its surface. In other words, body weight and surface do not vary in proportion with each other, and a mouse in relation to its weight has a larger body surface than a horse, and therefore loses, and has to make more heat.

Muscular work has an important influence upon the respiratory exchange, and this will be considered in the chapters on Nutrition and the Muscular System. Broadly, it increases both the CO_2 discharged and oxygen absorbed, though in experiments on the horse (Zuntz and Lehmann) it did not influence the respiratory quotient.

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* The question of the absorption of oxygen and the discharge of carbon dioxide is by no means so simple as might appear from these pages. Physiologists are not agreed as to whether the process is one of diffusion, or a secretion into the blood and an excretion from it. So difficult, indeed, is the problem, that those who have devoted years to its study declare it is beyond explanation in the present state of physical and chemical knowledge.

The influence of food on the respiratory exchange is very marked; during starvation it at first undergoes a marked decrease, and then remains constant. With food the exchange rises, the absorption of oxygen increases, and the output of CO_2 rises. Proteid food is much more energetic in this respect on a fasting animal than is a diet of fat.

Temperature has a marked influence on respiratory exchange, and this will be found dealt with in the chapter on Animal Heat.

Deficiency in Oxygen.—When an animal is compelled to breathe the same air over and over again, there is a gradual loss of oxygen and an increase in carbonic acid, and though death will ultimately ensue unless the air be renewed, it is remarkable that before this occurs nearly the whole of the oxygen will have been consumed from the atmosphere. This is further evidence, if any be needed, that the oxygen is not simply absorbed by the blood, and that its absorption does not obey the ordinary laws of pressure. Experimental inquiry has proved that animals may live in an atmosphere containing only 14 per cent. of oxygen, but that distress appears at 11 per cent., and rapid asphyxia follows when the oxygen falls to 3 per cent.

In poisoning by carbon monoxide the latter gas turns the oxygen out of the blood-cells, yet although the whole of the red-cells are converted into carriers of carbon monoxide, the animal may still be kept alive in an atmosphere of pure oxygen under pressure, the amount of oxygen dissolved by the plasma at an oxygen pressure of two atmospheres being sufficient to carry on the functions.

Hyperpnœa is the term applied to the slightly increased amplitude and frequency of the respiratory movements, such as occurs in gentle exercise, as the immediate result of any commencing defective oxygenation of the blood, or other cause which acts as a stimulus to the respiratory centre (see p. 108). When the stimulus is strong or continued, a further increase in the force and frequency of the respiratory movements takes place, and this condition is known as **dyspnœa**. The later stage of dyspnœa is characterized by the respiratory movements becoming 'convulsive' in their activity, and this finale to dyspnœa marks the onset of true asphyxia.

If the air supply be entirely cut off, asphyxia and death rapidly ensue. **Asphyxia** has been divided into three stages. In the first the attempts at breathing are laboured and painful, deep and frequent, and all the respiratory muscles, including the supplemental ones, are brought into play; convulsions occur, and the blood pressure rises. In the second stage the inspiratory muscles are less active, the expiratory still powerful, and the convulsions cease. In the third stage the animal lies unconscious, occasional violent inspiratory gaspings occur, the mouth is open (even in the horse), the pupils dilated, the pulse barely perceptible or absent; during this stage the blood pressure rapidly falls. Death occurs in from five to six minutes from the commencement of the first stage. Young animals are less easily asphyxiated than adults for the reason that their tissue respiration is much less; the length of time necessary to drown puppies and kittens is evidence of this, and they may recover even after prolonged immersion.

Excess of Oxygen.—When the excess of oxygen is considerable, viz., equal to a pressure of five atmospheres, warm-blooded animals die with convulsions. By increasing the amount of oxygen above that contained normally in air, the blood cannot be made to take up much more oxygen than if the normal amount only were present; a pressure of ten atmospheres only causes an increase of 3·4 per cent. absorbed, so that the blood contains 23·4 per cent. of oxygen instead of 20 per cent. The practical application of this fact in the treatment of certain diseases by the inhalation of oxygen is interesting. If we double the amount of oxygen in the air, less than 1 per cent. of the extra addition is absorbed. Either the small amount of extra oxygen thus absorbed must be very valuable, or we must find some other explanation of the undoubted advantage of oxygen inhalation in disease.

The physiology of the matter is, in effect, this: The air contains 20 per cent. of oxygen which is more than enough for the needs of the body; even the venous blood is returning to the lungs with from ten to twelve volumes of oxygen per cent. unused, while if the oxygen in the air be doubled less than 1 per cent. of the extra is absorbed. It may, however, be that the excess of oxygen in the alveolar air (see p. 99) of the lungs during oxygen inhalation, enables the tissues to obtain their normal amount more easily.

By **apnœa** is understood a standstill of respiration, no movement whether inspiratory or expiratory being made. Apnœic pauses may be produced experimentally by blowing air into and sucking it out of the lungs at a more rapid and forcible rate than the ordinary respiratory rhythm of the animal.

Something similar in appearance is witnessed in chloroform poisoning, and the term apnœa is frequently used *clinically* as synonymous with asphyxia. The physiologist uses it in another sense; apnœic pauses may be produced under conditions absolutely the reverse of asphyxia, as by rapidly and forcibly blowing air into the lungs. Under these conditions some observers suppose that a diminished irritability of the respiratory centre is produced as the result of hyper-oxygenation of the blood, though it is difficult to see how this condition is brought about. There is, on the other hand, good reason to think that repeated expansion of the lungs causes stimulation of the inhibitory fibres of the vagus, and so acts on the centre, and this view is supported by the fact that apnœa is difficult to produce after the vagi have been divided. A final view of the cause of apnœa assumes the normal stimulus to the respiratory centre to be CO_2 (see p. 112), in which case rapid inflation of the lungs would result in a more efficient removal of this gas, and thus to a diminution in the stimulus to inspiration. Possibly both this view and that of the inhibition of the centre by stimulation of the vagus fibres is correct, the two working concurrently.

The **Nervous Mechanism governing Respiration** is presided over by a centre in the medulla, the position of which in certain animals is very accurately defined, but which in general terms may be spoken of as being situated close to the deep-seated origin of the vagus and in front of the vasomotor centre. The respiratory centre was at one time considered to consist of an inspiratory and expiratory portion, but the present view is to regard the expiratory centre as doubtful; at any rate it cannot be localized, and though there are certain facts which suggest its existence, such as the act of straining in parturition, micturition, or defecation, still as compared with the inspiratory centre it occupies a very subordinate position. Hence it has been proposed to call the respiratory centre the 'inspiratory centre'; inspiration can only be carried out by rhythmical impulses from this region of the medulla, while there seems no doubt that expiration may be a purely passive act. It is believed that the respiratory centre is connected with every sensory nerve in the body, for the centre may be readily stimulated reflexly through sensory nerves, as an example of which may be quoted the sudden inspiratory gasp given when cold water is dashed on the skin.

But besides these there are special motor nerves wholly or almost wholly concerned in respiration with which this centre is closely in touch, for instance, the facial supplying the nostrils, the recurrent of the vagus which dilates the glottis, the phrenics which stimulate the diaphragm, the dorso-lumbar nerves which supply the intercostal and abdominal muscles. All these are interested in the production of that perfect and orderly sequence of events which beginning at the nostrils pass to the flank, and are so intimately concerned in the production of the respiratory rhythm.

The respiratory centre is *automatic*, that is to say, it is within itself that the discharges are generated which issue forth as inspiratory impulses; it is, indeed, as automatic as the heart, for if every nerve leading to it were divided the respiratory centre would still go on working. This view is not accepted by all physiologists, many of whom regard the stimulus to respiration as being a *reflex* one—viz., derived from without the centre. The centre consists of two halves, right and left, both of which work together yet may be shown experimentally to be capable of independent action. *Section of the cord* between the medulla and the phrenics leads to immediate cessation of all respiratory movements, excepting those of the mouth and nostril, which are anterior to the section, and hence to death from asphyxia.

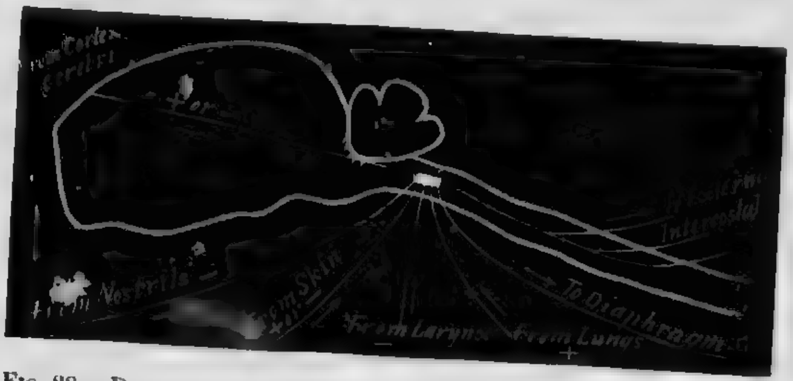

FIG. 28.—DIAGRAM TO ILLUSTRATE THE CHIEF NERVOUS CONNECTIONS OF THE RESPIRATORY CENTRE. (AFTER WALLER.)

The respiratory centre may be stimulated reflexly through any sensory nerve of which an example has previously been given. It is by no means necessary that the sensory nerves carrying impulses to the centre should be devoted exclusively to this function; probably the centre is linked up with all the cranial and spinal nerves.

The nature of the impulses issuing from the centre depend upon the character of the impulses which stimulated their production; thus the breathing may be controlled or even entirely stopped for a few seconds, or it may be hastened or slowed down, or quickened in rhythm, decreased in depth, or both rhythm and depth increased. From the brain impulses may pass to the centre which may cause an animal to increase its respirations as in sniffing, or to suppress them entirely, as when its head is under water. In the diagram Fig. 28 we have adopted Waller's symbols to signify an increase or decrease of respiration, and it will be seen that the cortex can supply either plus or minus influences. Another reflex path to the respiratory centre is that furnished by the nostrils through the medium of the nasal branch of the fifth nerve; through this channel principally minus influences are transmitted, viz., respiration is diminished. From the skin plus or minus influences may pass to the respiratory centre. A bucket of water dashed against a horse when the breathing is failing in chloroform narcosis will start an inspiration, and painful sensory impressions, as in 'firing,' greatly increase the respiratory movements. From the larynx important impulses pass to the respiratory centre through the superior laryngeal nerve. If this nerve be divided and the end in connection with the brain stimulated respiration is inhibited, in fact, if the stimulation be severe inspiration becomes weaker and weaker, and finally the breathing stops in expiration. This points to the superior laryngeal as stimulating expiration and inhibiting inspiration. The same result occurs with the sensory fibres of the glosso-pharyngeal supplying the pharynx. Here it is intimately connected with the act of swallowing, producing an inhibition of respiration the moment the epiglottis is pressed against the larynx.

Influence of the Vagus on Respiration.—The vagus is the most important afferent or ingoing channel to the respiratory centre; it covers the area from the glottis to the alveoli of the lungs.

If both nerves are cut the respirations become slower and deeper; if one nerve only is divided, this effect does not follow. Evidently, therefore, there are tonic impulses passing up the vagus which maintain the normal respiratory rhythm, which is lost when the nerves are divided. If the cut vagus be stimulated, using that portion still in connection with the brain, the respiration may be affected in at least two different ways; either all respiratory movements may partly or completely cease, or the rate of inspiration may be increased, and if the stimulation be powerful the respiration may stop in inspiratory tetanus. The interpretation of the results of these experiments is that two kinds of sensory fibres exist in the vagus which act on the respiratory centre; in what way they act is not fully agreed upon by physiologists.

Stating the case broadly the two kinds of fibres are regarded as inspiratory and expiratory, viz., fibres stimulating the inspiratory and expiratory portions of the centre respectively, and this view is necessary if it be held, as some authorities do, that respiration is a reflex act and not, as we have so far assumed, an automatic activity. Both sets of fibres are in alternate activity, and the question is, What is their normal stimulus? This has been determined to be due to the alternate distension and collapse of the air-vesicles, for experiment shows that if air be pumped into the lungs expiration is excited, and if it be sucked out inspiration is excited. Accordingly distension of the air-vesicles by the normal process of inspiration excites expiration, and contraction of the air-vessels in expiration excites inspiration. If, however, the respiratory centre is regarded as primarily automatic, the inspiratory set of fibres may be considered to increase the rate of respiration, the expiratory fibres as inhibiting or controlling inspiration, and thus producing expiration. If this view be adopted the act of inspiration proceeds from the automatic centre which requires no other stimulus than that which it generates within itself, while expiration proceeds from the stimulation caused by distension of the air-vesicles.

The nature of the internal stimulus to the respiratory centre has led to much discussion; it appears now to be generally accepted that the most important stimulus to its automatic action is the gases in the blood. Venous blood circulating through the centre causes the respiration to increase in force and rate, while blood containing a full amount of oxygen lowers the excitability; the respirations slow down, or even become suspended. Carbonic acid may be accepted as the chief stimulus to the respiratory centre.

Cause of First Inspiration.—At this point it is convenient to consider a question previously deferred (p. 89)—viz., What is the cause of the first act of inspiration in the fœtus? When the placental circulation is cut off, the respiratory centre of the fœtus becomes stimulated through the increased venous character of the blood now circulating through it. As a result of this, inspiration is automatically produced, but it is also assisted by reflex impulses carried from the surface of the skin due to handling and drying. Handling the skin of the fœtus while still *in utero* with the placental circulation intact may provoke respirations, and in all animals the very first act of the mother is to dry the fœtus and stimulate the skin by licking.

Division of the Phrenic Nerves.—We have referred to the cutting off of the respiratory centre by dividing the cord above the phrenic. If the cord be divided below the point of exit of the phrenics, the channel between the respiratory centre and lungs via the spinal cord is not interfered with, but the resulting paralysis of the abdominal and intercostal muscles necessitates that the action of the diaphragm should be more powerful. If one phrenic nerve be divided half the diaphragm is paralyzed, if both be divided the whole diaphragm is paralyzed and eventually undergoes fatty degeneration. Sussdorf states that division of the phrenic nerves in the horse leads to difficulty in breathing, increased heart action, and the collection of fæces in the rectum. In about twenty-four hours these symptoms pass away, and if the animal be worked no appreciable difficulty in breathing is subsequently observed.

Division of Seventh Pair.—Colin has shown that if the seventh pair of nerves be divided in the horse and the animal worked asphyxia results. This nerve dilates the nostrils; when divided the paralyzed flaccid nostrils are drawn inward at each inspiration and so close the opening.

The Amount of Air Required.—Numerous respiration experiments have been made on all animals, to determine the amount of air they require and the gases of respiration. The horse is of all others the one to which perhaps the greatest practical interest attaches in this respect, though a knowledge of it in connection with other animals is of value.

The lungs of a horse will contain about 1½ cubic feet (42·5 litres) of air at the end of a deep inspiration; during ordinary repose he draws into them between 80 and 90 cubic feet (2,265 to 2,548 litres) of air in the hour, though considerable variation may be found even in the same animal.

An average inspiration in the horse during repose amounts to about 250 cubic inches (4·1 litres), and the amount of air which flows in and out during ordinary quiet respiration is known as the *tidal air.* Speaking roughly it is only one-tenth of what the lungs can contain; the remaining nine-tenths are made up of *complemental, reserve,* and *residual air.* The complemental air is that over and above the tidal which can be taken in by a forced inspiration, while the reserve is a somewhat similar amount which can be expelled by a forced expiration. The most powerful expiratory effort is unable to remove from the lungs all the air they contain, and this amount is known as the *residual* air. The great variations which have been observed in the amount of air taken in by the same animals, under apparently identical conditions, cannot be adequately explained; the slightest disturbing influence alters both the rhythm and depth of the respirations. Under the influence of work the amount of air required is greater, and as a rule the faster the pace the more air needed;

but many disturbing factors occur which render experiments on this subject very contradictory, and productive of the greatest variation. During severe work, such as a gallop, a horse is taking air into his lungs to the extent of 850 cubic feet (24,067 litres) per hour at least, and probably more; the respirations from being 9 to 10 per minute during repose, may now be anything between 70 and 100 per minute. The effect of taking in all this extra air is that the *pulmonary ventilation* is increased; it is calculated that in man a deep inspiration more than doubles the capacity of the alveoli by distending them. In such paces as the canter, trot and walk, the amount of air used is correspondingly less; immediately the pace slackens or the horse stops the respirations at once fall, and the amount of air inspired becomes reduced. This is one of the great difficulties attending respiration experiments on horses under natural conditions.

A horse in a state of repose, according to Zuntz and Lehmann, produces 3 cubic feet (85 litres) of CO_2 per hour, and absorbs nearly 3½ cubic feet (99 litres) of oxygen; the expired air is found to have lost 4 per cent. of its oxygen and gained 3½ per cent. of CO_2. This is very much more than we found,* but it agrees pretty closely with the observations made on other animals and on man. It may be noted that even in animals which, from their small size or other causes, lend themselves to exactitude in experimentation, the most divergent results have been obtained, and the same thing is observed in man.

There are certain evident factors which considerably influence the amount of CO_2 produced and O_2 absorbed, and of these muscular work and the nature of the diet are the most prominent. As the result of muscular activity

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* 'The Chemistry of Respiration in the Horse during Rest and Work,' *Journal of Physiology*, vol. xi., 1890. It is now considered that samples of air are not sufficient to determine respiratory exchanges, the CO_2 has a tendency to accumulate in the tissues, and an apparatus which admits of prolonged observation is necessary, such as was employed by Zuntz and Lehmann. The apparatus employed in our observations is shown in Figs. 29 and 30.

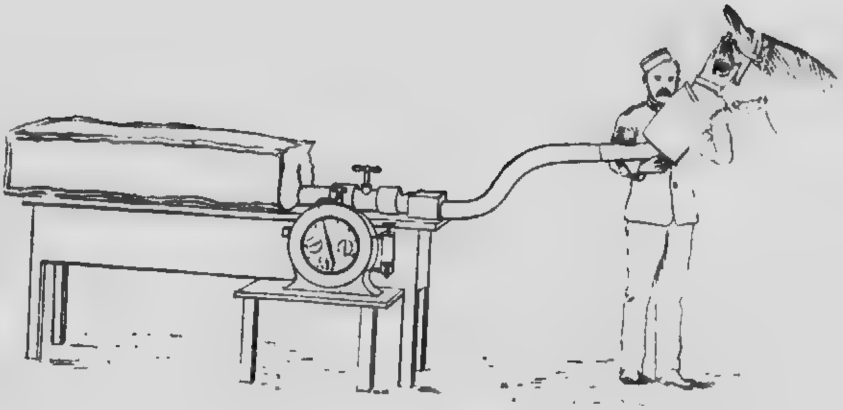

Fig. 29.—Horse in Position on Respiration Apparatus.

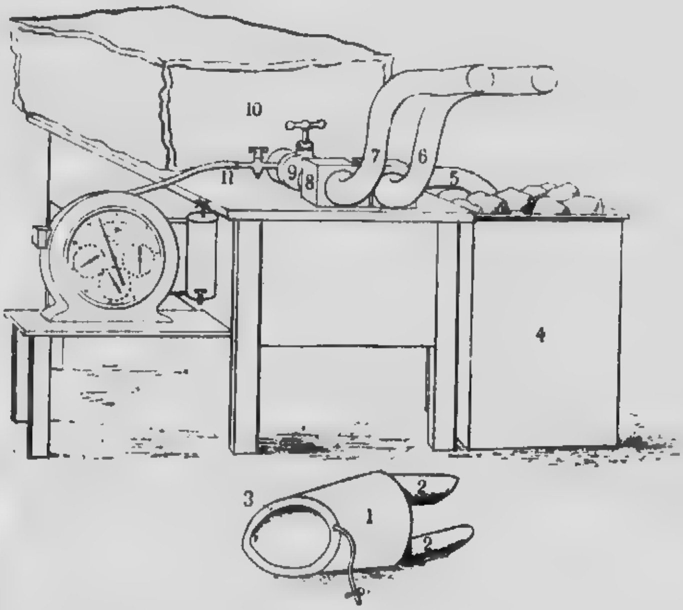

Fig. 30.

1, The face mask; 7, inlet tube to bag; 8, valve box through which the expired air passes to 10, a rubber bag of 20 cubic feet capacity. After an experiment the air is pressed out of the bag, and, passing through 11, is measured in the meter. 4, A chamber containing a tray of coke saturated with caustic potash, through which the inspired air passes and is robbed of its CO_2.

the production of CO_2 is increased; in the same way the amount of oxygen absorbed is greater, but experiment has failed to prove a definitely immediate relationship between the amount of oxygen absorbed and the amount of work produced. A diet rich in starch (carbo-hydrates) increases the amount of CO_2 produced, whilst fats have not such a marked effect in this direction. The respiratory quotient (p. 96) approaches unity in animals fed on a diet rich in carbo-hydrates, viz., there is very nearly as much CO_2 given off as O_2 absorbed; this is not the case with animals living on a flesh diet, where the respiratory quotient may fall as low as ·7.

The following table gives the amount of air respired and the gases of respiration for several animals; it is an old table by Boussingault. Recent observations on the horse, which we have previously quoted, give about half the values as compared to those assigned by Boussingault.

	Body Weight.	Amount of Air inspired in 24 hours.	Amount of Oxygen consumed in 24 hours.	Amount of Carbonic Acid produced in 24 hours.
		Cubic feet.	Cubic feet.	Cubic feet.
Horse ...	990 lbs.	3373	150	151·0
Cow	990 "	2782	122	122·3
Ass	330 "	1112	50	50·4
Pig	165 "	1216	54·7	55·1
Sheep ...	99 "	720	32·4	22·6
Dog	44 "	298	14·0	10·3

Alveolar Air.—We have indicated that the lungs cannot be completely emptied of air; a column of air even after death exists from the larynx to the alveoli of the lungs. The air in the air-sacs does all the work, and is known as the alveolar; from the air-sacs to the nostrils is the 'dead space' of the respiratory tract, and the composition of the air at any two parts of this space is not the same, it grows progressively poorer in oxygen in the direction of the lungs, and richer in carbon dioxide. During expiration the first air to leave is that from the 'dead space,' and the alveolar air follows towards the end of the expiration. During inspiration the incoming air is diluted with that already in the lungs, and its chemical composition at once alters. The air which distends the alveoli is therefore a mixture of air already in the alveolus combined with air from the bronchial passage, and the air in the bronchial passage, in its turn, becomes a mixture of bronchial air and air derived from the higher air-passages. How far the air of an ordinary inspiration travels is difficult to determine; under the most favourable circumstances some of the axial stream of the current might reach the alveoli, especially of the anterior lobes, but the bulk of it will get no further than the bronchi, and by so doing will have displaced and mixed with the air lately occupying the bronchi, now occupying the alveoli. In man it is estimated that in this way about one-eighth of the alveolar air is changed at each respiration.

Every endeavour has been made to ascertain the composition of the air in the alveoli of the lungs; if this could be put beyond doubt the vexed question of whether the gaseous exchange is due to diffusion or not would be capable of settlement. If, for instance, the pressure of carbon dioxide in the pulmonary capillaries was found to be the same as the pressure of this gas in alveolar air, diffusion would account for the exchange. The question is a very difficult one, but easier to settle from its carbon dioxide aspect than from the oxygen side. Haldane and Priestley, whose work we have closely followed, found in their experiments on alveolar air that under ordinary atmospheric pressure it contains practically a constant percentage of CO_2, and this is brought about by the influence of this gas on the respiratory centre. Carbon dioxide regulates the ventilation in the lungs, and thus provides the means for getting rid of itself; the more CO_2 in the blood the greater the alveolar ventilation.

Influence of Work on Respirations.—It is by no means clear why work causes an increase in the number and depth of respirations. Changes in the composition of the blood-gas stimulating the respiratory centre has been urged as a reason, but does not stand the test of experimental inquiry, for it is found that the blood leaving the heart during work is normal in composition. On the other hand, the evidence that the panting respirations of work are due to a 'something' produced in the muscles is very strong, for if the spinal cord of a dog be divided and the hind legs stimulated, increased respiratory movements are caused, just as if the animal had been running some distance. What the substance is is unknown; some observers have regarded it as sarco-lactic acid or acid phosphates, but nothing is definitely known, though it is interesting to observe that dilute acids injected into the blood give rise to the same condition. But hurried respirations may also be produced through the circulatory system. In an animal in training the breathlessness which it is one of the objects of training to get rid of, is due to the fact that more blood is brought to the lungs than can be disposed of. If the right heart pumps into the lungs more blood than the lungs can return to the left heart breathlessness follows. The gallop by which an animal gets its 'wind' and 'staying' power, operates through the circulatory system. Fortunately, the vessels of the lungs are capable of considerable adjustment, they hold more blood during inspiration than expiration, and in this way may be regarded as a safety valve to the heart. The important practical questions of work, 'condition,' and fatigue are again referred to in the chapter dealing with the Muscular System.

Air vitiated by Respiration was at one time believed to be poisonous, either on account of its deficiency in oxygen, its increase in carbon dioxide, or to the organic matter mixed up with it. Some modern investigators attribute the ill-effects of vitiated air mainly to the absence of free ventilation and the warm and humid atmosphere, by which the respiratory exchange and body metabolism are affected. Even the number of bacteria in the air is no guide to purity; there may be fewer in respired air than in the same air before respiration, in consequence of their being arrested in the lungs. On the other hand, Haldane and Lorrain Smith attributed the ill-effects of respiratory impurity to the excess of CO_2 and deficiency of O_2, hyperpnœa beginning when the CO_2 rises to 3 or 4 per cent.

The amount of air required for ventilation purposes is a question of hygiene, and reference should be made to works on that subject.

Respiratory Murmur.—An accurate acquaintance with the normal respiratory murmur is essential to the physician. The air-sounds both of inspiration and expiration should be heard all over the chest, the inspiratory murmur being louder and better marked than the expiratory; in fact, in many perfectly healthy chests the expiratory murmur can scarcely be heard. The normal murmur whether inspiratory or expiratory is soft in character; there is no harshness. The sound is best represented by the noise made by the stream of air which issues from a pair of hand bellows when gently blown.

The respiratory murmur, also known as the *vesicular murmur*, is caused by the friction of the air entering the alveoli. In those portions of the lung lying close to the bronchi and larger tubes there is, in addition to the vesicular murmur, a sound produced by the trachea and glottis. This is not distinct from the vesicular sound but is added to it, the result being that the respiratory murmur over the tubes is louder than elsewhere. The expiratory sound is weaker and shorter than the inspiratory, that is to say the sound is not continued to the end of expiration but dies away before that is reached. The expiratory murmur immediately follows the inspiratory without a pause, but there is a marked pause between the end of one expiration and the beginning of the next inspiration.

The ordinary murmur is best heard where the chest wall is thin; if the ribs be covered with fat or any great thickness of muscle the sound may be entirely lost. It is also important to note that there are some chests perfectly healthy where, for no apparent reason, the respiratory murmur is obscure or even undetectable.

Pathological.

Pneumonia and Pleurisy in the horse are very common in early life, and attended by a high mortality. The lungs and pleura, separately or combined, may suffer a degree of inflammation varying from small localized trouble, to general and extensive inflammation of the pleura and lungs. The whole of the lung tissue is never affected; even in the most severe cases of pneumonia there is some breathing area available: the upper portion of both lungs generally escapes. Effusion of fluid into the cavity of the thorax is a common sequel to pleurisy in the horse.

Both the above pathological conditions and their progress are determined by auscultation and percussion: there are many departures from the normal respiratory murmur, all of which have their significance.

Apoplexy of the Lungs arises as the result of overwork, especially in hot weather; but it may also occur in the winter. Horses ridden to death in the hunting field, in the name of 'sport,' die as a rule from pulmonary apoplexy; the lungs cannot get rid of their abnormal burden of blood to the left heart.

Bronchitis is probably rarely a disease distinct from pneumonia.

'**Broken Wind**' is one of the most interesting of the various chest diseases of the horse; it is a condition peculiar to this animal, liable to occur suddenly and frequently traced to errors in dieting. To state the case shortly the lungs lose their power of elastic recoil, and do not collapse even after death; the respirations are greatly increased, the expiratory effort being powerful and prolonged, a chronic typical cough becomes established, and the animal unfit for anything but slow work.

Roaring is a nervous affection, to which sufficient allusion is made in the section dealing with the larynx.

Spasm of the Diaphragm is another respiratory affection due to disordered nervous supply. The sound emitted is quite unlike that in the human; it appears to come from within the chest or abdomen, and is represented by a dull 'thud' like a magnified heart beat, which in its frequency and regularity it closely resembles, and for which it may easily be mistaken.

Rupture of the Diaphragm is a common lesion frequently due to disorders of the digestive canal, the gas generated in the intestine being sufficient to burst the diaphragm. Falls are by no means an uncommon cause; for example, an animal falls on to its head, and the abdominal viscera are propelled against the diaphragm. The diaphragm rarely gives way below, nearly always above, and in the tendinous substance rather than the muscular. This point is of physiological interest.

In the nasal passages the only affection of any moment is a collection of pus in the facial sinuses.

Laryngitis is frequently the result of strangles infection, or of ordinary cold. It presents no physiological features of interest.

In the ox pneumonia is rare, with the exception of the special highly infectious type, constituting one of the animal plagues. Practically none of the other diseases mentioned above as affecting the horse are found in any ruminant.

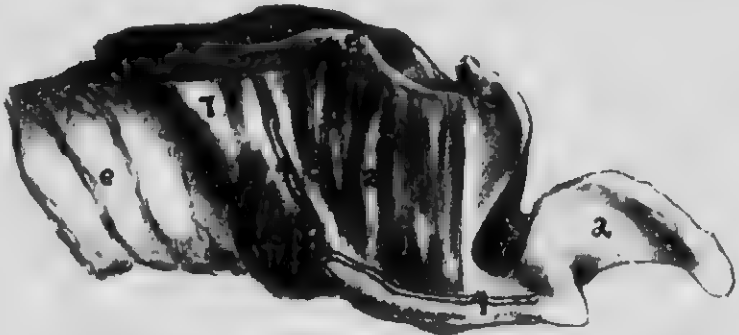

FIG. 31.—THE POSITION OF THE MUSCLES OF THE LARYNX IN THE HORSE.

a, Epiglottis; *b*, opening leading to the glottis; *c*, portion of the arytenoid cartilage; *d*, position of the joint formed between the cricoid and arytenoid cartilages; *e*, the trachea.

The wing of the thyroid cartilage has been removed so as to expose the constrictor muscles; 4, 4 represents its cut edge.

1 and 2, Thyro-arytenoideus: 1 anterior, 2 posterior fasciculus. The space between these two muscles indicates the position of the ventricle of the larynx. 3, Crico-arytenoideus lateralis. 5, Crico-thyroid muscle, the bulk of which lies inside the thyroid cartilage, and cannot, therefore, be seen. 6, Crico-arytenoideus posticus. 7, Portion of cricoid cartilage; the shaded portion in front of the figure represents where it and the thyroid meet. 8, Arytenoideus muscle.

SECTION 2.

The Larynx.

The larynx serves a twofold purpose, viz., respiration and phonation; in animals the former holds the more important position, the voice-producing function being of a very subordinate character.

The larynx may be described as a cartilaginous box placed at the summit of the trachea, the opening into it being capable of increasing or decreasing in size, and so allowing a larger or smaller amount of air to enter the lungs. Within the larynx are two elastic cords arranged V-shaped, the function of which is connected solely with the production of sound (Fig. 32). Both the respiratory and vocal functions require that the several parts of the larynx should move, viz., that the mouth of the organ should be widened or narrowed, or that the cords should be approximated, drawn apart, tightened or slackened. These movements are brought about by certain groups of muscles, those which approximate the walls of the glottis being known as the adductors, whilst those which widen it are known as the abductors.

The **Muscles of the Larynx** may therefore be divided into those of respiration and phonation (Fig. 31). As the most important feature in respiration is the opening or dilating of the glottis, the term respiratory muscle might be confined to the dilator of the glottis, while the constrictors would represent the vocal muscles; but the constrictors are not entirely without a respiratory function, as, for example, in coughing, so that in the following table they are included under this head.

Respiratory Muscles.

Dilator or abductor,	*Crico-arytenoideus posticus.*
Constrictors or adductors of the glottis,	*Crico-arytenoideus lateralis, Arytenoideus, and Thyro-arytenoideus.*

The crico-arytenoideus lateralis and posticus are direct antagonists; the lateralis depress the arytenoid cartilages and close the entrance into the glottis, the posticus swing the arytenoids upwards and outwards and enlarge the glottis.

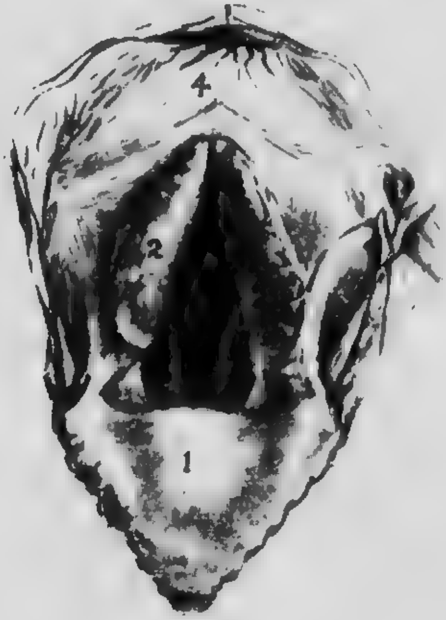

FIG. 32. –THE LARYNGEAL OPENING DURING ORDINARY RESPIRATION.

1, The epiglottis; 2, margin of arytenoids; 3, vocal cord; 4, pharynx laid open. The V-shaped slit is the glottis. Note how much wider the epiglottis is than the opening it has to cover.

Phonatory Muscles.

Muscle which relaxes the vocal cords,	*Thyro-arytenoideus*, anterior and especially posterior fasciculus.
Muscle which renders the cords tense,	*Crico-thyroid.*
Muscles which bring the cords together,	The respiratory adductors.
Muscle which moves the cords apart,	The respiratory abductor.

The entrance to the larynx is formed by the two arytenoid cartilages, the epiglottis, and the aryepiglottic folds; beyond these is the glottis proper, viz., the V-shaped opening formed by the vocal cords. When the laryngeal opening dilates, the vocal cords pass towards the wall of the cavity and render the V-shaped space wider; when the larynx closes the cords are approximated and the space rendered narrower (Figs. 32 and 33). During ordinary respiration there is very little if any alteration in the shape and

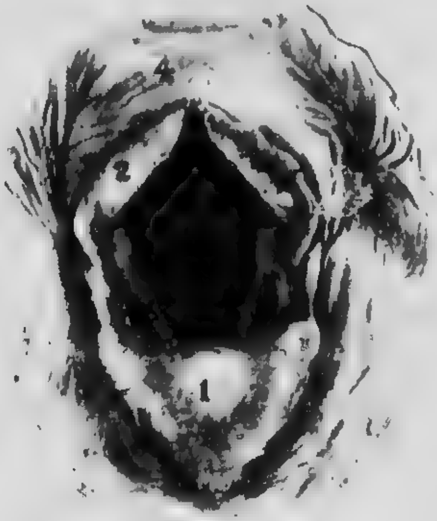

Fig. 33.—The Laryngeal Opening during Hurried Respiration, seen in a State of Dilation.

1, Epiglottis; 2, margin of arytenoids; 3, vocal cord; 4, pharynx laid open. Note the size and shape of the glottal opening as compared with Fig. 32.

size of the glottis; but during exertion every inspiratory movement is accompanied by an increase in size, every expiration by a decrease. At each expiration the vocal cords pass towards the centre line, and at each inspiration return to the wall of the larynx. The closure of the larynx, such as during the act of swallowing, is a powerful movement, and if the finger at this moment be introduced into the cavity and placed between the arytenoids, it experiences considerable pressure. The closure of the larynx is brought about by the depression and approximation of the arytenoid cartilages and the approximation of the vocal cords; in addition, during the act of swallowing the base of the tongue presses the epiglottis over the arytenoids and renders the part both air- and water-tight.

The **Epiglottis** is much larger than the opening it is intended to seal during a condition of laryngeal repose. It is carried backwards by the base of the tongue and pressed over the arytenoids; the larynx at the same moment advances, with its arytenoid cartilages closely approximated. After the act of swallowing the tongue advances, the larynx recedes, and the epiglottis returns to its position by means of its elastic recoil. It is not essential to a food- or water-tight condition of the larynx that the epiglottis should exist; it has been removed both by disease and experimentally, and its place is then taken by the base of the tongue. Nor is an arytenoid cartilage essential to safety in swallowing.

The **Nervous Mechanism of the Larynx** is peculiar. Sensation to the mucous lining membrane and motor power to the crico-thyroid muscle is supplied in the majority of animals by the superior laryngeal branch of the vagus, this nerve containing both sensory and motor fibres. In the horse the motor fibres running in the superior laryngeal are derived from the first cervical nerve and not from the vagus. All the other muscles both abductor and adductor are supplied with motor power by the inferior or recurrent laryngeal branch of the vagus. It is strange that both abductor and adductor muscles should have the same source of nerve supply, and one naturally asks what it is which determines that only the opening or only the closing muscles shall act at any given moment? No satisfactory explanation of this fact has been offered. All we know is that both dilator and constrictor fibres run in the recurrent laryngeal nerve and are quite distinct, and that in some animals the different bundles have been experimentally isolated and injured; injury to the dilator fibres producing abductor paralysis, and injury to the fibres going to the muscles which close the larynx producing adductor paralysis.

If the recurrent laryngeal be cut and the peripheral end strongly stimulated, the glottis almost invariably is found to close; in other words only the adductor fibres appear to be acted upon. If a *weak* stimulation be applied the glottis opens, viz., the abductor muscles are affected.

Another curious fact in the history of these recurrent nerves is furnished by pathology. In the disease of horses known as 'roaring,' there is paralysis of the left abductor muscle of the larynx, viz., the crico-arytenoideus posticus, the wasting and fatty degeneration due to paralysis being very marked. It is not unusual to find the adductor muscles normal in appearance, or presenting very little sign of disease, and even if pale and wasted the degree of degeneration cannot be compared with that furnished by the abductor muscle. This is a difficult fact to explain; one would think that as both abductor and adductor muscles receive the same nerve supply, equal wasting would occur in both groups. Again, it is observed when the recurrent has been divided experimentally, that the abductor muscle loses its irritability long before the adductors, and the same fact may be observed in *post mortem* stimulation of the nerves. If the recurrent laryngeal nerves be divided under ether, and the peripheral ends stimulated, adduction of the larynx is obtained; but if the ether narcosis be pushed to a dangerous extent and the nerves then stimulated the larynx dilates, that is abduction follows. These and other observations have furnished a law which is of clinical significance, viz., that in *functional* disturbance of the larynx the adductor muscles are first affected, but that in changes accompanied by organic lesions the abductor muscles are the first to suffer.

When one recurrent laryngeal nerve is divided the vocal cord on that side remains immovable and therefore cannot approach its fellow; the healthy cord endeavours to compensate for the weakness of its companion by passing beyond the middle line of the larynx, in its attempt to come into contact with it.

The inspiratory distress occasioned in 'roaring' is not brought about, as has been described, by a paralyzed vocal cord flapping about, for the elastic nature of the cord and other reasons negative this. The sound is produced by the paralyzed left arytenoid being drawn into the glottis at each inspiration, which is the explanation why the noise which accompanies the disease is always inspiratory and never expiratory.

Phonation.—Voice is produced by the approximation and vibration of the vocal cords, the pitch of the voice being produced by the tension of the cords, whilst the quality is due to the shape of the cords, viz., their thickness or thinness. The position of the resonant chambers such as the mouth, pharynx, posterior nares, and even nasal chambers also importantly affects the quality of the voice. It is obvious that the chief alterations in the larynx during phonation refer to the vocal cords; these are approximated by the adductor muscles, and separated by the abductor muscles, whilst they are relaxed by the thyro-arytenoideus and tightened by the crico-thyroid. The latter muscle has a peculiar action, it lowers the thyroid cartilage on the cricoid and swings the wing of the thyroid outwards, thus rendering the cords tense. These changes in the vocal cord produce changes in the shape of the V-shaped glottal opening; in a high note the glottis is reduced to a mere slit, in deeper notes the cords are separated. If air be forced through the larynx of a dead horse and the tension of the cords altered, a sound remarkably like a neigh may be produced. The ventricles of the larynx and cavities of the mouth, nose, pharynx, etc., act as resonators. Being filled with air, they effect the needful alterations in the quality of the voice and assist in giving it its distinctive character; thus the false nostrils furnish the 'snort' of the frightened or 'fresh' horse, the nasal chambers the whinny and neigh of pleasure, the mouth and pharynx the neigh of impatience, loneliness, excitement, etc. We do not consider that the guttural pouches act as resonators, and Colin obtained no alteration in the character of the neigh by opening them.

The voice of each class of animal—horse, ass, ox, sheep, and pig—is so distinctive that we may recognise their presence without seeing them; yet though the larynx in all these animals differs more or less, the difference is not sufficient to offer any explanation as to why the sounds it emits are so entirely distinct. The voice of male and female animals differs in intensity. The wild neigh of the stallion is very different from the neigh of the mare, and the bellowing of the bull is distinct from the 'lowing' of the cow. The operation of castration has a remarkable effect on the voice, the neigh of the gelding resembling that of the mare.

In the horse the voice is used during sexual and ordinary excitement, also during fear or especially loneliness, during pain, anger, and as a mark of pleasure. It is not possible to convey in words the difference in the notes produced, but they are easy to recognise. The horse is essentially a sociable animal; when accustomed to be in the company of others he dislikes separation, and shows it by persistent neighing, which is perhaps more noticeable amongst army horses than any others. The neigh of pleasure is often spoken of as the 'whinny'; the word rather conveys an idea of the sound made. Sounds which can only be described as 'screams' are often evoked during 'horse-play' and temper, or by mares during œstrum. It is not a scream as we know it in the human subject, but no other word conveys an idea of its shrillness. If a horse cries from pain (which is very rare), as during a surgical operation, the cry is a muffled one and short; it is a groan rather than a cry.

In the cerebral cortex voice is represented in the præcrucial and neighbouring gyrus of the dog, and corresponding regions in other animals. Stimulation of this region leads to *bi-lateral* adduction of the cords; it is curious why stimulation of one side of the brain should lead to movements of both vocal cords. There is no region of the cortex of the dog which leads to abduction of the cords, though such a region is found in the cat. The cortical centre communicates with a subordinate centre in the medulla situated in the region of the fourth ventricle, and stimulation of certain parts of this centre leads to abduction and of others to adduction of the cords.

Neighing in the horse is produced by an expiration, partly through the nostrils and partly through the mouth; **braying** in the ass is both inspiratory and expiratory, nostrils and mouth each taking a share in it. The ventricles of the larynx are large in the horse and relatively still larger in the ass and mule; they act as resonators and allow of free vibration of the vocal cords. According to Chauveau both ass and mule have the subepiglottic sinus provided with a thin membrane capable of vibrating. In the ox, sheep, and goat, the larynx is very simple, there are only rudimentary vocal cords and no ventricles. The **bellowing** of the ox and **bleating** of the sheep are expiratory efforts through the mouth. The dog and cat have a larynx something like that of the horse, but the ventricles are shallow; the voice is produced almost entirely through the mouth, though both growling and purring may occur through the nostrils.

Yawning is a deep slow inspiration followed by a short expiration; the air, even in the horse, is taken in by the mouth, which is widely opened and the jaws crossed.

Sneezing and **Coughing** are expiratory efforts. The former occurs solely through the nose and, excepting in the dog and cat, is unaccompanied by the peculiar sound attending this act in the human subject. If snuff be introduced into the nostrils of the horse, a peculiar though well known vibration of the nostrils occurs as if the animal were blowing its nose, and this is, in fact, what it accomplishes. It is an entirely nasal sound, the mouth takes no share in the act. Coughing occurs through the mouth, the long palate in the horse being raised for the purpose. Before coughing can occur the lungs must be filled with air and the glottis closed; a forcible expiration follows, the glottis opens, and the air is expelled through the mouth.

Hiccough is due to a sudden contraction of the diaphragm. While the air is rushing into the lungs the glottis closes, and the incoming air, striking the closed glottis, produces the sound. The condition known as spasm of the diaphragm in the horse is very different from a human hiccough, and has been referred to more fully on p. 120.

CHAPTER V

DIGESTION

SECTION 1.

Digestion in the Mouth.

Prehension of Food. — The methods by which animals convey food to the mouth differ according to the species. In the horse the lips play an important part, for which purpose they are thick, remarkably strong, and endowed with acute sensation; in the ox they serve a subordinate function, being rigid and wanting in mobility; in the sheep the upper lip is cleft in such a manner as to divide it completely into two parts, each possessing independent movement; in the pig the lower lip is pointed and the upper one insignificant.

In manger feeding the horse collects the food with the lips, but in grazing cuts off the grass with the incisor teeth, drawing the lips back in order that they may bite closer to the ground. In the ox the tongue is protruded and curled around the grass, which is thus drawn into the mouth and taken off between the incisor teeth and the dental pad. In the sheep the divided upper lip allows of the incisors and dental pad biting close to the ground, so that animals of the sheep and goat class can live on land where others such as the horse and ox would starve. In whatever way the food is cut off, it is carried back by the movements of the tongue to the molar teeth, there to undergo a more or less complete grinding.

In the ox and sheep the incisor teeth move freely in their sockets, the object of which is to prevent injury to the dental pad, for which purpose also they are placed very obliquely in the jaw. In the horse the incisor teeth in early life are very upright but become oblique with age. The molars in all herbivora are compound teeth; in the horse they are very large, especially those in the upper jaw. Being composed of materials of different degrees of hardness they wear with a rough surface, which is very essential to the grinding and crushing they have to inflict on grasses and grain. The teeth in herbivora, both incisors and molars, are constantly, though slowly, being pushed out of the sockets which hold them; in this way wear and tear is compensated for, whilst the fang of the tooth becomes correspondingly reduced in length. It is owing to this fact that the incisor teeth alter in shape and direction, and so enable the age to be determined. The tables of the molar teeth are not flat but oblique; this is

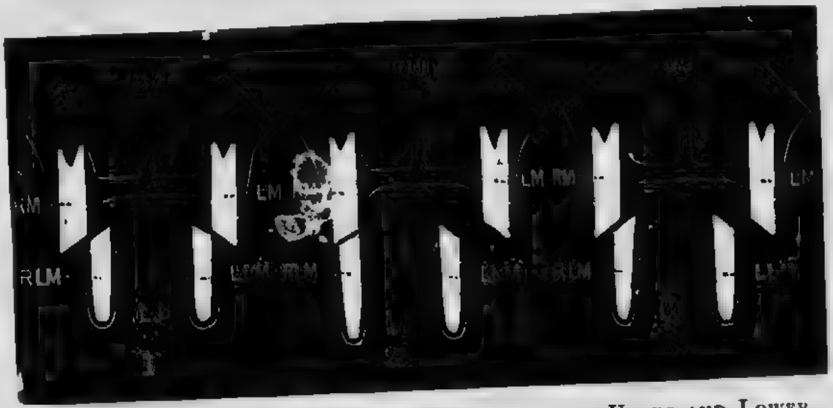

FIG. 34.—SCHEMATIC TRANSVERSE SECTION OF THE UPPER AND LOWER JAWS OF THE HORSE BETWEEN THE THIRD AND FOURTH MOLARS, SHOWING THE POSITION OF THE TABLES OF THE TEETH DURING REST AND MASTICATION.

UJ upper jaw, LJ lower jaw, RM right molar, LM left molar, RLM right lower molar, LLM left lower molar. 1, The position of the teeth during rest, the outside edge of the lower row in apposition with the inside edge of the upper. 2, The jaws fully crossed masticating from right to left; the tables of both upper and lower molars now rest on each other. 3, The position half way through the act of mastication; the outer half of the lower teeth wearing against the inner half of the upper.

especially well seen in the horse where the cutting surface is chisel shaped, the upper teeth being longest on the outside, while those of the lower row are longest on the inside (see Fig. 34). This arrangement produces sharp teeth, which are a constant source of trouble and loss of condition in horses.

The movements of the tongue are important. In the ox and dog they are very extensive, the former animal having no difficulty in protruding the tongue and even introducing the tip into the nostrils. It is not a very common habit with horses to protrude the tongue except when yawning, but they have considerable power in withdrawing it in the mouth. A great difference exists between the tongue of the horse and that of the ox; the former is flabby, broad and flat at the end, constricted opposite the frenum, and swells out at the apex; it is comparatively smooth on its surface. The tongue of the ox narrows from base to apex, the latter being pointed; it is very rough, which prevents it from losing its hold on the food, protects it from such injury as might be inflicted by coarse grasses, and is also of value to the animal in cleaning its body. The tongue is supplied with motor power by the hypoglossal nerve and with sensation by the lingual branch of the fifth, which supplies the anterior two thirds of the mucous membrane, the posterior third being supplied by the lingual branch of the glosso-pharyngeal; the same nerve also supplies the sense of taste to this part of the organ, while taste for the anterior two thirds is supplied by the chorda tympani of the seventh pair.

The inside of the mouth of the ox is covered with long papillæ, which look backwards; these would appear to be of use in preventing the food from falling out of the mouth. In the horse no such papillæ exist, in fact the lining membrane of the part is remarkably smooth. The majority of animals have grooves in the palate; they are well marked in the horse, ox, sheep, and even in the dog. Their function is probably connected with assisting the tongue to pass the food back in the mouth.

Drinking is performed by the animal drawing the tongue backwards and thus using it as the piston of a suction-pump; this action produces a vacuum in the front of the mouth, as the result of which the cheeks are drawn inwards, the lips at the same time being closed all round, excepting a small space in front which is placed under water. Such is the method in both horse and ox; in the former animal the head is extended while drinking, the ears are drawn forward at each swallow and during the interval fall back. The cause of this motion is not clear, but is probably due to the movement of air in the guttural pouches. Lapping in the dog is performed by curling the tongue in such a way as to convert it into a spoon. Sucking, like drinking, is produced by the animal creating a vacuum in the mouth by closing the lips, decreasing the size of the tongue in front and increasing it behind, the dorsum being applied to the roof of the mouth. The foal places the tongue beneath the nipple and curls it in from each side; by this means he protects it from the lower incisors and gets a better hold.

Mastication is performed between the molar teeth; the movements which the jaws undergo, to admit of this being carried out, depend upon the class of animal. In the dog they are very simple, being only a depression and elevation of the jaw; this motion means a simple temporo-maxillary articulation, and such is met with in this animal. In the horse and ox the movement is not only up and down, but lateral, and some say even from front to rear. This necessitates a complex joint capable of affording a considerable amount of play, and this is provided by a disc of cartilage being placed between the articulation, which accommodates itself to the varying movements of the joint in the horse, ox, and sheep, and also saves the part from jar. In herbivora, therefore, we find the cartilage extensively developed, whilst in carnivora it is small and simple. The character of the movement occurring in the temporo-maxillary articulation of herbivora during mastication is as follows. During rotatory movement, or lateral displacement, one of the articulating heads remains as a fixed point simply turning on its centre, whilst its fellow describes an arc; this is why the movement can only occur on one side at a time (Gamgee). During mastication the contents of the orbital fossæ are observed in the horse to be alternately ascending and descending. This movement is due to the coronoid process of the lower jaw, the fossa being pushed up as it comes forward and depressed as it recedes. The muscles which bring about this important lateral movement of the jaws, which in the ox, owing to the freedom of the articulation, may be termed rotatory, are the two pterygoids, especially the internal. The herbivora can only masticate on one side at a time; when tired on one side the process is reversed and the opposite molars take on the crushing. It is surprising the length of time an animal will carry on mastication on one side; even as long as an hour has been observed in the horse by Colin. Gamgee noticed that in the ox the first stroke of the molars is in the opposite direction to the regular action which follows; thus if masticating from right to left the first stroke is made from left to right. It is important to note that in those animals where a single-sided lateral or rotatory movement in mastication is necessary, the upper jaw is always wider than the lower; this we can understand, for if both were the same width the molar teeth would not meet each other when the jaws were crossed for lateral mastication. This extra width of the upper over the lower jaw, in conjunction with the peculiarity of mastication, explains why the molar teeth of the horse and other herbivora wear with sharp chisel edges (see Fig. 34).

In the horse mastication is slow and as a rule well performed; he takes from five to ten minutes to eat one pound of corn, and fifteen to twenty minutes to eat one pound of hay. In the ox mastication is imperfectly performed to start with, but the material is eventually brought back to the mouth by the process of rumination, and undergoes thorough re-mastication. In the dog mastication is imperfectly performed; after a few hasty snaps of the jaw the material is swallowed.

Opening the mouth is equivalent to depressing the lower jaw, for the upper takes no share in the process. The muscles which open the mouth are comparatively small, for very little effort is required, the *sterno-* and *stylo-maxillaris* and *digastricus* perform this function. On the other hand, the closing of the jaws in mastication is a difficult task, and for this purpose very powerful muscles exist, they are the *masseters*, *temporals* and *pterygoids*. In the dog the temporal muscles are considerably developed, whilst in herbivora the masseters are the largest.

The nerves employed in mastication are the sensory fibres of the fifth which convey to the brain the impulse resulting from the presence of food in the mouth, while the motor fibres of the same nerve supply the needful stimulus to all the muscles of mastication excepting the *digastricus*, which receives its motor supply from the seventh pair.

The process of **Deglutition** is usually described as occurring in three stages. The first stage practically comprises carrying the food back to the base of the tongue and pressing it against the soft palate; it is a simple process and readily understood. In the second stage the act is complex, for the bolus or fluid has to cross the air passage and must be prevented from falling into the nasal chambers, or finding its way down the trachea. To accomplish this the soft palate is raised and so closes the nasal chambers, the tongue at the same time being carried backwards, while the larynx and pharynx are advanced. This movement causes the base of the tongue to press on the epiglottis and close the larynx, which is further secured by the arytenoid cartilages and vocal cords coming close together. The bolus or fluid can now safely pass towards the pharynx, being grasped tightly by the pharyngeal muscles and pressed into the œsophagus. In the third act of swallowing the food is carried down the œsophagus by a continuous wave of contraction, which starts at the pharynx and ends at the stomach. Chauveau points out that owing to its extreme length, the soft palate of the horse passes completely into the pharynx during the second act of deglutition. The length of the soft palate prevents food or water being returned by the mouth when once they have entered the pharynx, so that in vomiting, or in cases of sore throat, the food, water, or other material is returned by the nostrils.

The action of the epiglottis in the closure of the glottis has been much discussed. We have described it as being forced over the opening by the base of the tongue and the advancing larynx; but the epiglottis is not essential to swallowing, for an animal can swallow when it has been removed, and even when one of the arytenoid cartilages has been excised. With a finger in the larynx it can easily be demonstrated that the part tightly and forcibly closes during the second stage of swallowing, the vocal cords and arytenoids being brought so close together that the glottis is perfectly air-tight. It has been pointed out that animals usually swallow with a flexed neck, as in this position the epiglottis is behind the soft palate and in the most favourable position to be applied over the glottis; it has also been shown that when the head is extended the epiglottis is in the mouth, viz., anterior to the soft palate. We have found it in this position in the horse, and judging from the fact that in a state of nature the horse and ox swallow with an extended and not with a flexed neck, it is probable that in feeding off the ground the epiglottis is anterior to the soft palate. During the third stage of deglutition the bolus can be seen slowly travelling down the channel of the neck; if liquid however be passing, the movement is very rapid, for as many as sixty swallows may be made in a minute. Both in eating and drinking the third act of deglutition can occur against gravity; this is because it is a muscular act. The whole process of deglutition is considerably assisted by the salivary secretion. When this has been experimentally diverted swallowing only occurs with difficulty and very slowly.

The œsophagus of the horse is found to differ considerably from that of most other animals. It is composed for the greater part of its length of red striated muscle, while at and near its termination the previously thin muscular coat becomes very thick and rigid, and the red gives way to pale non-striped muscle; further, the lumen of the tube becomes very narrow. The thick terminal end of the œsophagus of the horse is always closely contracted, so that if cut through close to the stomach no material can escape; this is one explanation why horses vomit with such difficulty. In the ox, sheep, and dog, the tube is composed of red muscle throughout; it terminates in a dilated end at the stomach, and owing to its thin distensible walls even bulky material can pass along it; what the ox and dog can swallow with ease would certainly 'choke' the horse.

The first stage of deglutition is voluntary, but the remaining processes are quite involuntary, and are brought about by the stimulation of a centre in the medulla known as the swallowing centre. By means of ingoing or afferent nerves supplied by branches of the fifth and the superior laryngeal, the centre is made acquainted with the fact that food is present in the fauces. A reflex act is now set up in the centre and an impulse conveyed to the muscles of the part by outgoing or efferent nerves, furnished by the pharyngeal plexus (composed of the vagus and glossopharyngeal) to the constrictor muscles of the pharynx, by the hypoglossal to the tongue, and by the recurrent laryngeal to the muscles which close the glottis. The glossopharyngeal is the inhibitory nerve of deglutition; if the central end be stimulated it is impossible to produce the act of swallowing. Swallowing may be induced without the presence of food in the fauces; touching the rim of the glottis will produce it, as also will pouring fluids into the trachea, or even touching the interior of the trachea as far down as the bronchi. The swallowing centre also presides over the œsophagus, and the peristaltic wave from the pharynx to the stomach is produced by impulses sent out from this centre through the vagus. This wave is, therefore, not due to the nerve handing on a contraction by direct conduction from one layer of the muscular wall of the œsophagus to the next. Hence, when once started it is not arrested either by ligaturing or dividing the œsophagus, though section of the œsophageal nerves prevents it. It is not uncommon in watching a bolus pass down the neck of the horse to see it suddenly come to a standstill, and then slowly pass on again after probably an attempt to ascend. This is generally due to absence of saliva. In rumination and in vomiting the wave runs upwards from the stomach to the pharynx.

The Saliva.

During the process of mastication the food becomes mixed in the mouth with a fluid known as saliva, the secretion of which occurs in three distinct pairs of glands. The method by which it is formed is important to understand, as much the same process occurs in other secretory glands which we have not the same opportunity of watching during their activity.

Classification of Salivary Glands.—The three glands which secrete saliva are the parotid, submaxillary, and sublingual; these are structurally divided into two groups, mucous and serous (or albuminous) glands, the submaxillary and sublingual being types of the first, the parotid the type of the other. The salivary glands in the herbivora are of considerable size, the submaxillary and sublingual being well developed in the ox, while in the horse they are rudimentary. According to Colin, there is no relationship between the weight of the glands and the amount of fluid they secrete; the parotid in all cases secretes more than the others. In the horse it is only four times heavier than the submaxillary, but it secretes twenty-four times as much saliva; in the ox the parotid is not so large as the submaxillary, but its secretion is four or five times greater.

Amount of Secretion.—Colin places the daily secretion of saliva in the horse at 84 lbs., and in the ox at 112 lbs., though the amount will depend on the dryness of the food consumed; thus hay absorbs more than four times its weight of saliva, oats rather more than their own weight, and green fodder half its own weight.

Physical and Chemical Characters.—Mixed saliva is an alkaline, opalescent, or slightly turbid fluid which readily froths when shaken. On standing exposed to the air it throws down a deposit of carbonate of lime due to the loss of its carbonic acid. It has a specific gravity of 1005 in the horse, and 1010 in the ox. Examined microscopically saliva is seen to contain epithelial scales and salivary corpuscles. The latter are small round granular cells which seem to be altered leucocytes and are probably derived from the soft palate. About ·6 per cent. of the saliva consists of mineral matter, and ·2 per cent., more or less, of organic matter, the latter consisting of mucin (which gives saliva its well-known viscidity and ropiness), and small amounts of proteid substances the nature of which has not been exactly determined. Mucin belongs to a peculiar group of proteid bodies combined with a carbohydrate, for which see Appendix. Ptyalin or salivary diastase is the most interesting organic constituent of saliva in man, but it is doubtful if it exists in the herbivora, and under any circumstances its amount has not been determined. Ptyalin is also absent from the saliva of the dog. The salts of saliva are principally carbonate of lime, alkaline chlorides, and phosphates of lime and magnesia. A substance known as sulphocyanide of potassium has been found in minute quantities in the saliva of the human subject, but is absent from that of the horse. The gases of the saliva are principally carbonic acid, with traces of oxygen and nitrogen; there is no body fluid which contains so much carbonic acid as saliva (65 vols. per cent.). The three salivas have different physical properties:—Parotid saliva is watery, clear, and free from mucin, but contains a small quantity of proteid; submaxillary and sublingual saliva are viscid, especially the latter. In man the parotid saliva is rich in ptyalin.

Colin has observed certain peculiarities in the secretion of saliva in herbivora which deserve careful attention.

He demonstrated that the secretion from the parotids is unilateral, the gland on that side of the mouth on which the animal is masticating secreting two or three times as much as its fellow; the submaxillary and sublingual glands, on the other hand, secrete equally, no matter on which side mastication is being performed. Further, the parotids secrete during rumination, the unilateral secretion still being maintained, whilst the submaxillary and sublingual glands are during this process in a state of rest. In a fasting horse the parotids are quiescent, while in the ox they are active. Observations tend to show that in the former animal during fasting the mouth is kept moist by secretions from the sublingual, palatine, labial and molar glands. The glands of the mouth are extensively developed in the horse, particularly the palatine, and some large ones close to the epiglottis; their secretion is extremely viscid. Neither the sight of food nor the introduction into the mouth of sapid substances, produces any effect on the salivary secretion from the parotid of the horse; sapid

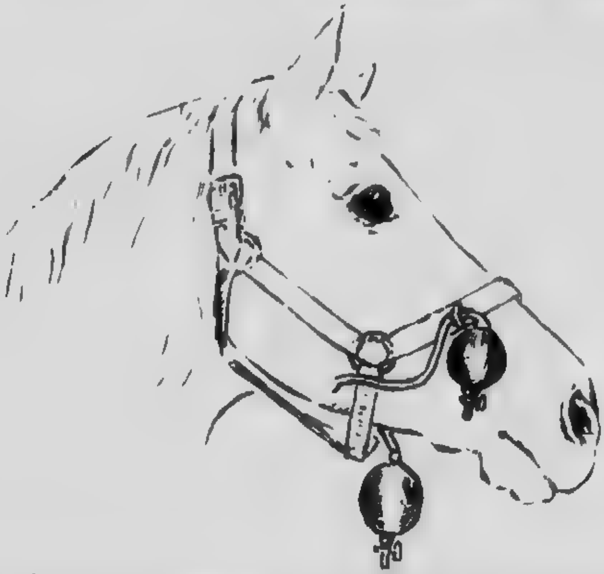

Fig. 85.—Apparatus employed by Colin in Experiments on the Secretion of Parotid and Submaxillary Saliva.

substances, however, stimulate submaxillary secretion. The apparatus used in these experiments is shown at Fig. 35.

The **use of the saliva** in herbivora is to assist in mastication and swallowing, stimulating the nerves of taste, and in ruminants assisting in rumination. According to our observations on the horse, saliva has no chemical action on the raw starch of its food, and this is not surprising when we remember that the starch grains are enclosed in an envelope of cellulose, a substance on which saliva has no action. So intimately, however, is salivary secretion associated with starch conversion, that it is not possible to pass over without further notice the action produced on starch in man, and according to some observers in horses and cattle, by the presence of ptyalin in the saliva.

The **starch** found in plants exists in the form of granules possessing a shape peculiar to the species, these granules are enveloped in a tough envelope of cellulose; before the true starch, the *granulose* contained in the cellulose envelope, can be reached the cellulose must be traversed. For this reason some animals, like man, cannot digest raw starch, but by cooking, the starch (granulose) is liberated and free to be acted upon; on the other hand, the herbivora are capable of digesting raw starch, perhaps because they can digest cellulose.

If boiled starch be mixed with filtered human saliva and kept at a temperature of 95° F., in a short time the characteristic reaction of a blue colour with iodine disappears, and a reddish colour is formed on the addition of this reagent, indicating the presence of a substance known as **erythrodextrin.** At this time the fluid which before was sugar-free, now contains distinct evidence of its presence; by continuing the action of the saliva it is shortly found that the red colour on the addition of iodine has disappeared, and the fluid gives evidence of containing a considerable proportion of sugar. But analysis shows that for the amount of starch employed the full amount of sugar has not been obtained; in other words, there is a second substance present besides sugar, which is produced as the result of the action of the saliva, and to this the name **achroodextrin** has been given; it is formed from erythrodextrin. The sugar formed from starch by the action of saliva is not grape-sugar but maltose; glucose (dextrose or grape-sugar) only being found in small quantities if at all. This action of the saliva on starch is described as the **Amylolytic** action; it is due to the presence of **Ptyalin** which plays the part of a ferment. The process is permanently destroyed by a high, inhibited by a low temperature, retarded by a slightly acid or alkaline medium, and destroyed by free hydrochloric acid. If starch be boiled with a dilute acid, conversion into sugar occurs. The difference between the action of boiling acid on starch and of saliva is that the latter can only produce maltose whereas the acid produces dextrose.

The view we hold as to the non-amylolytic action of saliva in herbivora is not supported by other observers: Ellenberger * distinctly states that both the parotid and submaxillary secretions of the horse and ox can convert starch into sugar, but in the case of the horse it is only the saliva first secreted by the glands after a rest which possesses this property; as secretion proceeds the power is nearly lost. In the pig, according to this observer, all the salivary glands are starch converting; in the rabbit the submaxillary has no action while the parotid is energetic; in the cat, dog, horse, sheep, and ox the action is very feeble or entirely absent. Meade Smith † states that the saliva of the horse will convert crushed raw starch into sugar in fifteen minutes, and that the process is continued in the stomach; he further adds that the saliva of the horse will convert cane into grape-sugar. In ruminants he believes starch conversion takes place both in the mouth and rumen. Though we do not accept these views, we shall shortly endeavour to show how starch is converted into sugar in the stomach of the horse. It is interesting in this respect to note that in man starch conversion, brought about by the action of ptyalin, is also now recognised as taking place in the stomach from the swallowed saliva, in fact, that the bulk of the conversion takes place there, and not in the mouth.

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* 'Physiologie der Haussäugethiere.'

† 'Physiology of the Domestic Animals.'

Secretion of Saliva.—The mechanism concerned in the secretion of saliva deserves careful attention, for the reason that it throws considerable light on other secretory processes. The subject has been worked out by so many competent observers that the leading points are beyond all doubt; the submaxillary gland of the dog has afforded the desired information, and there is reason to believe that the same process holds good for the parotid and other glands, both of this animal and of herbivora.

The chief point in the secretion of saliva is that it is controlled by the nervous system, and is not directly dependent upon any mere increase in the blood pressure in the gland. Afferent nerves, viz., the gustatory division of the fifth and the glosso-pharyngeal, convey from the mouth to the medulla a certain impulse, which by means of efferent nerves is conveyed to the gland and secretion results. The efferent nerve of the submaxillary gland of the dog is supplied by the **chorda tympani**, a small branch given off by the seventh cranial nerve, which enters the gland at its hilum and supplies the vessels with dilator and the cells with secretory fibres. The second nerve supplying the submaxillary gland is a branch of the sympathetic, which spreads out and invests with constrictor fibres the walls of the artery supplying the part (Fig. 36). Thus the chorda tympani supplies the gland with secretory fibres and the walls of the vessels with dilator fibres, while the sympathetic supplies the vessels with constrictor fibres, and only a few secretory fibres.

If the tongue or the lingual branch of the fifth or glosso-pharyngeal nerves be stimulated secretion of saliva results; if the sympathetic nerve be divided and the tongue then stimulated secretion follows, but if the chorda tympani be previously divided no secretion follows on stimulation of the tongue, lingual, or glosso-pharyngeal nerves. If the chorda be stimulated the vessels dilate, the gland becomes red, the blood flowing from the veins is arterial in tint, and the veins pulsate; in addition to this, there is an abundant secretion of watery saliva poor in solids. When the sympathetic is stimulated, exactly the reverse is observed—viz., the vessels constrict, in consequence of which the gland

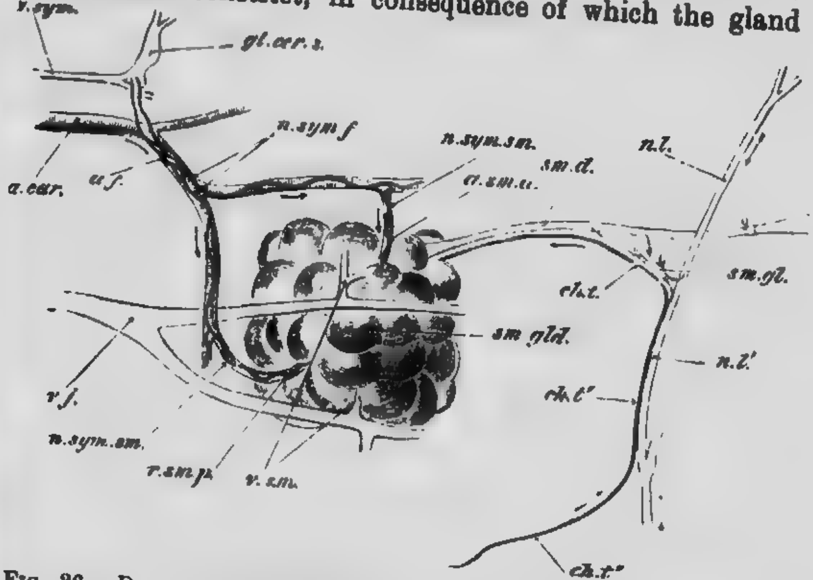


FIG. 86.—DIAGRAMMATIC REPRESENTATION OF THE SUBMAXILLARY GLAND OF THE DOG WITH ITS NERVES AND BLOODVESSELS (FOSTER).

(The dissection has been made with the animal on its back, and is very diagrammatic.)

The submaxillary gland (*sm. gld.*) occupies the centre of the figure; the bloodvessels supplying it, derived from the carotid artery *a.car.*, are seen on the left, whilst the duct from the gland *s.md.*, in which a canula is inserted, is on the right of the figure.

The chorda tympani nerve *ch.t''.*, running in company with the lingual branch of the fifth *n.l'.*, is seen to the right and below; after running together the two nerves separate, the chorda tympani *ch.t.* running along the submaxillary duct to the gland. Close to where the two nerves separate is the submaxillary ganglion *sm.gl.*

The sympathetic nerve supply is shown in the figure to the left and above, the fibres being derived from the superior cervical ganglion *gl.cer.s.* and coursing along the bloodvessels to enter the gland.

The bloodvessels leading from the gland fall into the jugular vein *v.j.*

The arrows indicate the direction of the nervous impulses during the reflex act, ascending to the brain by the lingual and descending by the chorda.

becomes pale, only a small quantity of extremely viscid saliva flows which is rich in solids, the blood in the veins becomes very dark in colour, and the blood-stream slows to such an extent that if the veins leading from the gland be cut, the flow from them is less than from a gland at rest. That the increased flow of blood to the gland produced by stimulating the chorda is not the essential cause of the secretion, is proved by the fact that the pressure of the saliva in the duct of the gland is higher than the blood pressure within the vessels. Further, if before stimulating the chorda some atropin be injected, stimulation of the nerve still produces to the full all the vascular changes, but not a trace of saliva is secreted. Hence, secretion is not due merely to increased blood pressure. This atropin experiment proves the existence in the chorda of two sets of nerves, viz., secretory and vaso-dilator; owing to the action of atropin the secretory nerves are paralysed, whilst the vaso-dilators are not. And in the sympathetic two sets of nerves can similarly be demonstrated, secretory and vaso-constrictor, though it is most likely that in the majority of animals the secretory fibres in the sympathetic are few in number. Pilocarpin is antagonistic to atropin and produces a profuse flow of saliva.

A peculiar phenomenon is observed in connection with salivary secretion after division of the chorda. Though the gland is cut off from its secretory nerve, yet one or two days after section a secretion appears, and may continue for some weeks until the gland undergoes atrophy. This is known as 'paralytic secretion.'

Heidenhain's view of the action of secretory nerves is that a gland is supplied with a trophic or nutritive nerve which excites the formation of the organic constituents of the secretion, and a secretory nerve which controls the secretion of water and inorganic salts. The cranial nerves are chiefly secretory, whilst the sympathetic are trophic, hence stimulation of the chorda gives a watery saliva poor in solids, whilst stimulation of the sympathetic gives a scanty saliva rich in solids.

The method by which secretion in the parotid gland is carried out differs in no essential respect from that of the submaxillary. The nerves supplying the parotid are the glosso-pharyngeal (the action of which corresponds to the chorda of the submaxillary) and the sympathetic. In the glosso-pharyngeal are dilator fibres, and in the sympathetic constrictor fibres for the bloodvessels, while both trunks contain secretory nerves.

It will be observed that no reference has been made to the nerve ganglia in connection with salivary secretion. Ganglia are a collection of cells in the course of a nerve. If these cells be paralysed by nicotine, as was first shown by Langley, stimulation of the nerve does not produce a secretion.

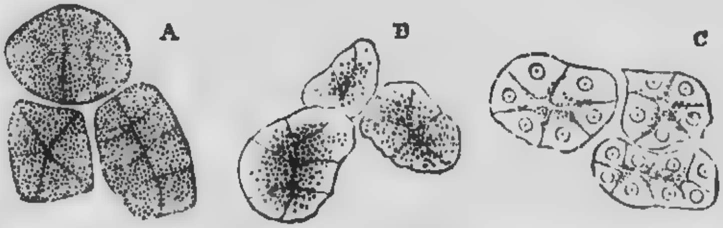


FIG. 37.—CHANGES IN THE CELLS OF THE LIVING PAROTID (SEROUS GLAND) DURING SECRETION.

A, At rest; B, in the first stage of secretion; C, after prolonged secretion (Foster, after Langley).

The **changes occurring in the cells** of the salivary glands during secretion depend upon the type of gland. We will therefore describe separately, from Langley's observations, the changes in the cells of a serous gland such as the parotid, and in those of a mucous gland of which the submaxillary is a type. We select Langley's observations, since he examined the living gland and not one simply hardened and stained. During the stage of rest in a living serous gland, the cells are found to be filled with a quantity of granular material, and the outline of each individual cell is indistinct; the lumen of the gland is also occluded, and no nucleus can be observed in the cells; in other words, the gland is charged with its secretory products (Fig. 37, A).

During activity the cells get rid of their granular material, which gradually passes towards the centre of the acinus or lumen, leaving each cell with a clear outer edge, whilst that edge next the lumen is still granular (Fig. 37, B). In an exhausted condition the cells are smaller and remarkably clear, only a few granules being left in them on the inner edge, whilst the lumen is now distinct and large, and the nuclei are clearly seen occupying a central position (Fig. 37, C).

If a mucous gland at rest be examined under like conditions, the cells are found filled with granules much larger

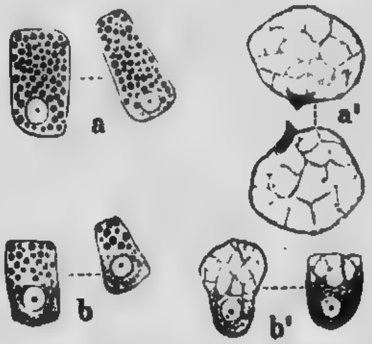


FIG. 38.—CELLS FROM MUCOUS GLAND (SUBMAXILLARY GLAND OF THE DOG). (FOSTER.)

a, From loaded gland; b, from discharged gland; a′, b′, treated with dilute acetic acid; a′, from loaded; b′, from discharged gland.

than those of a serous gland, and a nucleus is seen occupying one edge of the cell (Fig. 38, a). During activity the granules are passed into the lumen of the gland, but they do not leave behind them in the cells the same clear space seen in the serous cell (Fig. 38, b). If the cells, while in an active condition, be acted upon by water or dilute acetic acid, the granules swell up and become transparent owing to the mucin they contain, and a delicate network is seen to pervade the cell (Fig. 38, a′). A similar appearance is produced in the exhausted cell (Fig. 38, b′), excepting that less transparent mucin is seen and more granular substance, while the nucleus of the exhausted irrigated gland is seen passing towards the centre of the cell instead of remaining close to the outer wall. Though we have spoken of these granules as mucin, in the gland they are not really mucin, but the mother substance of it, viz., *mucigen*, which during the act of secretion is converted into mucin. The same holds good for the serous type; the granules in the resting gland are the precursors of the ferment or the *zymogen* of the secretion, from which the secretion is actually formed at the moment it is poured out.

The outcome of the changes above described proves that the organic elements found in the salivary secretion are manufactured by the cells in the glands; the inorganic constituents are either the result of filtration or secretion. Experiments made by Langley and Fletcher go to prove that even water and salts are the result of an act of cell secretion, and not of mere transudation.

SECTION 2.

Stomach Digestion.

Important digestive changes in the food of the lower animals take place in the stomach. It is not a matter for surprise to find that the size and shape of this organ varies with the species of animal; we should expect to meet with a simple stomach in the dog, and complex arrangement in vegetable feeders. It seems remarkable that any animal should possess a laboratory capable of converting grass, hay, and grain into muscle and fat; and it is evident that the conversion of vegetable into animal tissues must be a more complex process than the conversion of animal tissues into the living structure of an animal body. But it is curious to observe that a complex stomach for a vegetable feeder is by no means a necessity; the stomach of the ruminant and the simple stomach of the horse could not be in greater contrast, whilst the resulting laboratory processes are practically identical. So far as vegetable food is concerned, it does not matter whether the solution and absorption of its readily soluble matters comes before maceration, or whether maceration precedes the extraction of the readily soluble substances. If maceration comes first, as in ruminants, bulky gastric compartments are provided for the purpose, and the subsequent intestinal canal is small. If the simple stomach comes first, bulky intestines for the purpose of maceration follow; in both cases ample provision is made for the maceration necessary for the solution of the cell wall and fibrous portion of plants. The dog with its simple stomach and simple intestines offers no difficulty to our understanding. He lives on flesh and converts it into flesh; it is not very clear why he has both a stomach and intestines, for the whole process of digestion is simple, and could be readily carried out single-handed by the intestines. In fact, the stomach of the dog has been removed experimentally and the animal remained in health.

For simplicity in construction the stomach of the dog occupies one end of the scale, for complexity the gastric reservoirs of the ox occupy the other, whilst between the two comes the stomach of the omnivorous pig, partaking of some of the characters of the carnivora and ruminant and belonging to neither.

Stomach Digestion in the Horse.—The subject of stomach digestion in the horse has been worked out by means of feeding experiments, as it has been found impossible to establish a gastric fistula in this animal owing to the distance the stomach lies from the abdominal wall; pure gastric juice has, therefore, never been obtained from the horse.

The first peculiarity to be noticed in soliped digestion is that the stomach is rarely empty; it is only when horses have purposely been deprived of food for not less than twenty-four hours that an empty stomach can be obtained. On the other hand, feeding experiments show that very shortly after food arrives in the stomach it commences to pass out, and the difficulty thus presented to the observer in reconciling these opposed facts is at first sight considerable. It is perfectly true that food does pass out early, it is equally true that it is long retained, these opposite conditions being the result of the periods of digestion. When food enters an empty stomach it passes towards the pylorus, where it meets with a fluid of an alkaline or neutral reaction which has come from the mouth. As more food is consumed an acid fluid is secreted in the stomach, and material commences to pass out at the pylorus into the bowel, the amount passing out not equalling at present the amount passing in. Thus the stomach becomes gradually distended, and when two-thirds full, which is the condition in which the most active digestion occurs, the amount passing out will, if more food be taken, equal the amount being swallowed, so that we have a stream of partly peptonized chyme streaming out of the right extremity, while a corresponding bulk of ingesta is entering the inert left sac. In fact, the stomach may during feeding allow two or three times the bulk of food to pass out which remains in it when the meal is finished. Let us now suppose that the 'feed' is finished. At once the passage of chyme into the duodenum ceases, or becomes so slowed down that only small quantities of food pass out, and so gradually does this occur that it will be many hours before the stomach is really empty, though had the process continued as it commenced, it would not have contained anything at the end of an hour. This condition of stomach digestion in the horse may be variously modified, depending on the nature of the food, the quantity given, the form in which it is given, the order in which one food follows another, and whether water be given before or after feeding. All these are points requiring our attention, but before giving it we must briefly look at the stomach itself.

The mean capacity of a horse's stomach is, according to Colin, from 25 to 30 pints, or from ·5 to ·63 of a cubic foot; these figures were obtained from a very large number of observations, and give the extreme size of the organ when distended; the viscus is under the best conditions for digestion when it contains about 17½ pints, or is distended to two-thirds of its capacity. The mucous membrane of the stomach of the horse is peculiar; one portion of it, practically half, is a continuation of the membrane of the œsophagus, this ends abruptly and is succeeded by the villous coat which extends to the pylorus. It is in this latter coat that a true digestive juice is secreted, though not from the entire surface, for on examining the villous membrane it is found to differ greatly in appearance, the

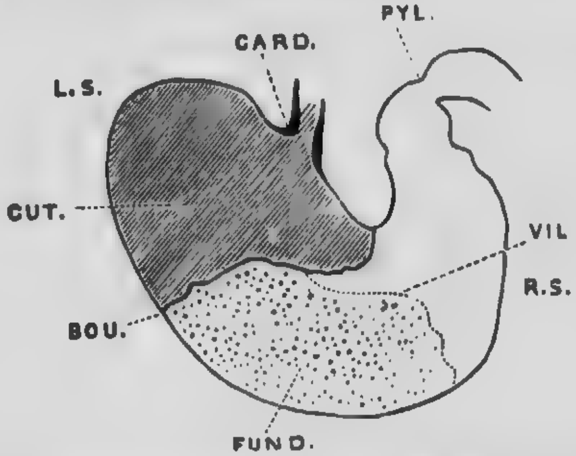


Fig. 39.—Longitudinal Section of the Stomach of the Horse.

CARD., Cardia; PYL., pylorus; L.S., left sac; R.S., right sac; CUT., cuticular coat; VIL., villous coat; BOU., boundary line between the cuticular and villous portions; FUND., fundus of the stomach. The dotted surface indicates the area for the secretion of gastric juice.

fundus being channelled, furrowed, and velvety, whilst the pyloric portion is smooth. It is in the fundus only where true gastric juice, viz., pepsin and acid, is secreted; in the smooth pyloric mucous membrane only pepsin is formed. The area of the fundus-secreting surface is about one square foot. Fig. 39 shows the relative position of the various parts of the mucous membrane of the stomach of the horse; the drawing accurately indicates the shape of the stomach, the position of the inlet and outlet, and the direction and position of the various areas. A very remarkable amount of mucin is secreted by the villous sac of the stomach, and forms over the inner surface of the viscus a thick gelatinous firmly adherent coating like white of egg, which cannot be washed away even by a powerful jet of water.

The pyloric orifice of the stomach is usually large and open, and there is a distinct pyloric ring; behind this the duodenum is dilated, and the gut comports itself in such a singular manner (which has a very important bearing on the pathology of the organ) that mention must be made of it here. From the pylorus the duodenum curves down and then up again, forming a letter U; so much does this remind one of a well-known form of trap used in drainage, that we have described it as the syphon trap of the duodenum (Fig. 40). The use of this trap appears to be to regulate the passage of material from the stomach into the intestines. Our observations have shown that its presence in all probability influences rupture of the stomach, for the more distended the large bowels become, the greater the pressure exercised on the duodenum, and in cases of severe tympany the passage from the stomach to the intestines is completely cut off. Should fermentation still continue in the stomach, the contents can neither escape into the œsophagus, nor into the bowel, and the coats of the viscus

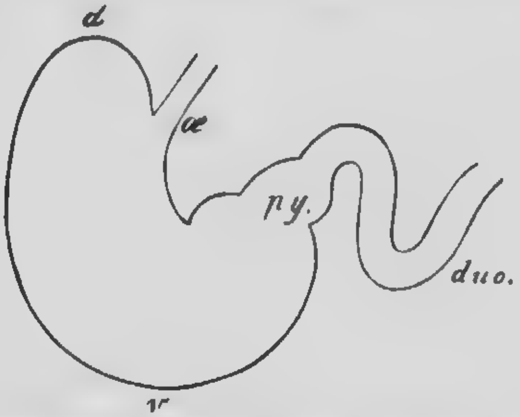


Fig. 40.—Longitudinal Section of the Stomach of the Horse, showing the Syphon Trap of the Duodenum.

œ, Œsophagus; *py.*, pylorus; *d*, left sac; *v*, fundus; *duo.*, duodenum.

may be completely ruptured under the intense strain. It was mentioned on p. 138 that the œsophagus of the horse near its termination changes from red to pale muscle and for several inches increases enormously in thickness. It is this thickened contracted end of the œsophagus which completely seals the stomach anteriorly; nothing can be forced out by this passage, not even after death or under great pressure.

The physiological points of interest in the structure of the horse's stomach are: 1, that it is small; 2, that it is not in contact with the abdominal wall, but rests on the colon; 3, that the outlet and inlet are situated close together; 4, that the cardia is tightly contracted; 5, that only a portion of its surface is capable of secreting a digestive fluid; 6, that there are remarkable differences in the character and nature of the various regions of its mucous membrane.

We can now consider the stomach digestion of the two chief foods used for horses, viz., hay and oats.

Digestion of Hay.—Hay, as we have shown, mixes in the mouth with four times its bulk of saliva, and after a very perfect grinding passes into the stomach. If the stomach be empty it is of no size and the material lies in the pyloric region; as the viscus gradually fills, the gastric juice begins to act, and chyme commences to pass into the intestines probably in a very imperfectly elaborated form. Assuming the animal to have finished eating the hay, we now find the output into the intestine becomes small and slow. The gastric juice has an opportunity of acting more thoroughly upon the ingesta, which turn yellow on that surface which is in contact with the villous wall, the compression of the stomach on the contents causing them to become distinctly moulded into a mass the shape of the viscus. Owing to gravity there is more fluid towards the pylorus than elsewhere, and for the same reason the greater curvature in all probability is fuller than the lesser. The material in the stomach is perfectly comminuted, resembles firm green and yellow fæces, and the smell is peculiar, like sour tobacco. The yellowness is due to the gastric juice, and is consequently more marked towards the pylorus; the portion coloured green is the part as yet unacted upon by the juice. The entire surface of the stomach and its contents are now acid, excepting at the cardia, where it may occasionally be alkaline from swallowed saliva; the acidity is greater at the fundus than at the cardia. This general acidity shows that a diffusion of the gastric juice must have been going on. There is no evidence of any churning motion, the cake-like condition into which the hay is compressed, in spite of its four equivalents of saliva, is due to the compression of the material by the stomach walls.

The duration of stomach digestion of hay is variable, but we quote one or two of Colin's experiments. A horse received 5½ lbs. of hay which he took two hours to eat; at the end of that time he was destroyed, and the stomach contained 2·2 lbs.; thus in two hours he had digested 3·3 lbs. Another horse received 5½ lbs. hay, and was destroyed three hours from the time of commencing to feed; in the stomach were found 1·54 lbs., so that in three hours this horse had digested 3·96 lbs. In the third hour (during which time he was not feeding), judging from the first experiment, he had digested only ·66 lb., whereas the previous rate of digestion for the first two hours was at the rate of 1·65 lbs. per hour.

To return to our previous statement, when the animal is no longer feeding the rate of digestion at once becomes reduced, and it is probable that several hours must elapse, assuming no further food be given, before the stomach completely empties itself. This period may be fifteen, eighteen, twenty-four or even thirty-six hours. We starved a horse for twenty-four hours, and at 6 a.m. gave him 6 lbs. of dried grass; he was destroyed at 3 p.m., and the stomach still contained 2½ lbs.; in nine hours, therefore, only 3½ lbs. had been digested. In another observation carried out under similar conditions, only 1 lb. had been digested in four hours and three-quarters. Of 4 lbs. hay given only 1 lb. 11 ozs. were digested in six hours; of

3½ lbs. hay, 2¼ lbs. were digested in five and a half hours; while in another observation, of 4 lbs. hay, 2 lbs. 12 ozs. were digested in five hours.

Colin's elaborate researches furnish us with very complete data on the question of hay digestion in the horse. He fed fourteen horses on hay, and destroyed two of them at regular intervals; each animal received 5·5 lbs. of hay, and digestion was counted from the time they were fed. Here are the results:

AMOUNT OF HAY GIVEN 5·5 LBS.

	lbs.		lbs.
After 2 hours, the first horse had digested	3·87 ;	the second,	3·08
,, 3 ,, ,, ,,	3·88	,,	4·24
,, 4 ,, ,, ,,	4·04	,,	3·56
,, 5 ,, ,, ,,	4·32	,,	5·08
,, 6 ,, ,, ,,	4·10	,,	4·55
,, 7 ,, ,, ,,	4·01	,,	4·35
,, 8 ,, ,, ,,	4·37	,,	4·44

From this it is seen that the rate of digestion during the first two hours is rapid and then falls off, so that even at the end of eight hours there is still something left in the stomach. The second horse in the five hours' observation had very nearly digested the whole of the ration, but this is an exception. There is no doubt that it is extremely difficult to get the stomach to empty itself. We fed a horse on dried grass and destroyed it eighteen hours later; there was still a small quantity of food in the stomach. In another case the stomach, after fifteen hours, was found empty. In a third case a horse was given grass twice at intervals of twenty-four hours; he was destroyed eighteen hours after eating his last feed, and a handful of grass was still found in the stomach.

Digestion of Oats.—We have now to consider the digestion of oats, and here again we still observe the same fact noted under that of hay, viz., that the stomach commences to pass its contents into the intestine during feeding, and that this slackens considerably when no more food is entering the viscus. Colin fed six horses on 5·5 lbs. of oats each, and destroyed them at certain intervals.

	lbs.		*lbs.*
After 2 hours, one horse had digested	2·7 ;	a second,	2·5
" 4 " " "	3·1	"	3·4
" 6 " " "	3·5	"	3·0

We have observed in a horse which had received 2 lbs. of oats, and was destroyed twenty hours later, that the stomach had not completely emptied itself. In another experiment four hours after feeding on one pound of oats, 6 ozs. were recovered from the stomach.

A horse received *lbs. oats.*	And was destroyed in *hours.*	Amount digested *lbs.*	*ozs.*
4	4	2	3
3	4½	1	11¼
4	4	2	4
3	3¾	2	2¼
3	4	—	
4	4	1	13½
3	6½	2	6½
4	4	3	0
4	4	0	12

The last horse is included to illustrate a point of some importance in the feeding of animals. For eighteen months this horse had never tasted corn, having been fed on a patent food; a sudden change in diet is the explanation why he only digested 12 ozs. of oats in four hours. It will be observed that the fifth horse in this series digested nothing, even at the end of four hours; we can only account for this by the fact that the animal was in a strange place where the feeding experiment was carried out, and was of a very nervous disposition.

Arrangement of Food in the Stomach.—An interesting practical and physiological study is the effect of feeding horses on different foods in succession. When hay is given first and oats afterwards, the hay is found close to the greater curvature and pylorus, and the oats in the lesser curvature and cardia; no mixing has occurred, both foods are perfectly distinct, and a sharp line of demarcation exists between them (Fig. 41, I.). During digestion mixing occurs at the pylorus but nowhere else; no matter what compression the contents have undergone as the result of gastric contractions, the foods always remain distinct. The presence of the oats, however, causes the hay to pass out more rapidly than it would have done had it been given alone. Colin observed that half the hay, but only one-fourth or one-sixth of the oats, would, under these conditions, pass into the intestine in two hours. Ellenberger has shown that when hay and oats are given in this order, a portion of the oats may pass out into the bowel by the lesser curvature without entering either the left sac or fundus of the stomach (see Fig. 41, I.). When oats are given first, followed by hay (Fig. 41, II.), the oats commence to pass out before the hay, but the presence of the hay causes the oats to pass more quickly into the intestines than they otherwise would have done. If a horse be fed on three or four foods in succession they arrange themselves in the stomach in the order in which they arrived, viz., they do not mix. The first enters the greater curvature, the last the lesser curvature, and it is only at the pylorus that any mixing occurs under ordinary conditions (Fig. 41, III.). This regular arrangement of the different foods in layers is only disturbed when a horse is watered after feeding; under these circumstances the contents are mixed together and digestion thereby impeded. Apart from this, the influx of a considerable quantity of fluid into a stomach already containing as much as it should hold, means that material is washed out of it into the small and large intestines, and this may set up irritation and colic. By watering a horse after feeding more than half the food may at once be washed out of the stomach. The water which a horse drinks does not remain in the stomach, but passes immediately into the small intestines, and in the course of a few minutes finds its way into the cæcum; hence the golden rule of experience that horses should be watered first and fed afterwards. We may summarise these facts by saying that in a succession of foods the first consumed is the first to pass out. That does not mean to say that the whole of it passes out before any portion of the succeeding food enters the bowel,

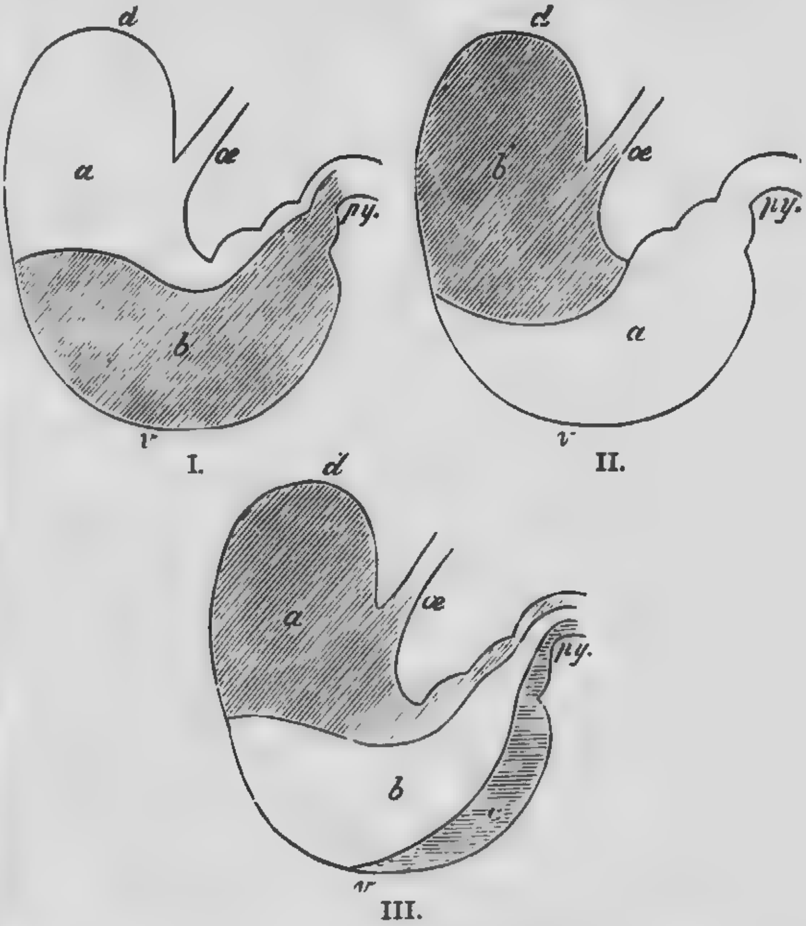


Fig. 41.—Longitudinal Section of the Horse's Stomach, showing the Arrangement of the Food according to the Order in which it was received (Ellenberger).

In each case *œ* is the œsophagus; *py*, pylorus; *d*, the left sac; *v*, the fundus. I. Hay first, followed by oats: *b*, the hay; *a*, the oats; the latter are passing along the lesser curvature and escaping with the hay at the pylorus. II. Oats first, followed by hay: *a*, the oats; *b*, the hay. III. The order of three successive feeds; *c*, the first feed; *b*, the second; *a*, the third.

for we have shown that after a time, at the pylorus, they mix and pass out together; but the actual influence of giving a food first is to cause it to pass out first. The practical application of this fact, according to Ellenberger, is that when foods are given in succession, the least albuminous should be given first. This appears to distinctly reverse the English practice of giving oats first and hay afterwards, but perhaps only apparently so, for experiment shows that the longer digestion is prolonged, the more oats and the less hay pass out, so that some hay (under ordinary circumstances a moderate quantity) is always left in the stomach until the commencement of the next meal. The presence of this hay from the previous feed may prevent the corn of the succeeding meal from passing out too early. According to Ellenberger, in order that horses may obtain the fullest possible nutriment from their oats, hay should be given first *and then water;* this carries some of the hay into the bowel and after a time the oats are to be given. The remaining hay now passes into the bowel and the oats remain in the stomach. This does not accord with English views of watering and feeding horses, which have, however, stood the test of prolonged practical experience.

The **appearance of the food after it has been in the stomach** depends upon the period of digestion. We have previously drawn attention to the fact that an hour or two after hay has been taken the material is found in a finely chopped condition, firm, one may almost say dry, in places, though towards the pylorus it is liquid. This hay contains between four and five parts of saliva; it is yellow in colour where the gastric juice has attacked it, but of rather a greenish tint elsewhere, and it has a peculiar odour. Several hours after feeding, the stomach is found to contain a variable quantity of watery fluid discoloured by the hay which is left behind, part of which may be found floating on the fluid. At other times, when the stomach is empty, the fluid is viscid, contains numerous gas bubbles, and is of an amber or yellow tint; this particular fluid is no doubt saliva and mucin, with possibly a little bile, the result of a reflux from the bowel. When oats alone have been given the contents of the stomach are found liquid, the fluid being creamy in consistency and colour; the oats are swollen, soft, and their interior exposed; towards the end of digestion the creamy fluid is replaced by the frothy yellow one. With both hay and oats, and also other foods, there is a peculiar sour-milk-like smell from the contents of the stomach, more marked with bran and oats than with hay, the latter, as previously mentioned, smelling like sour tobacco.

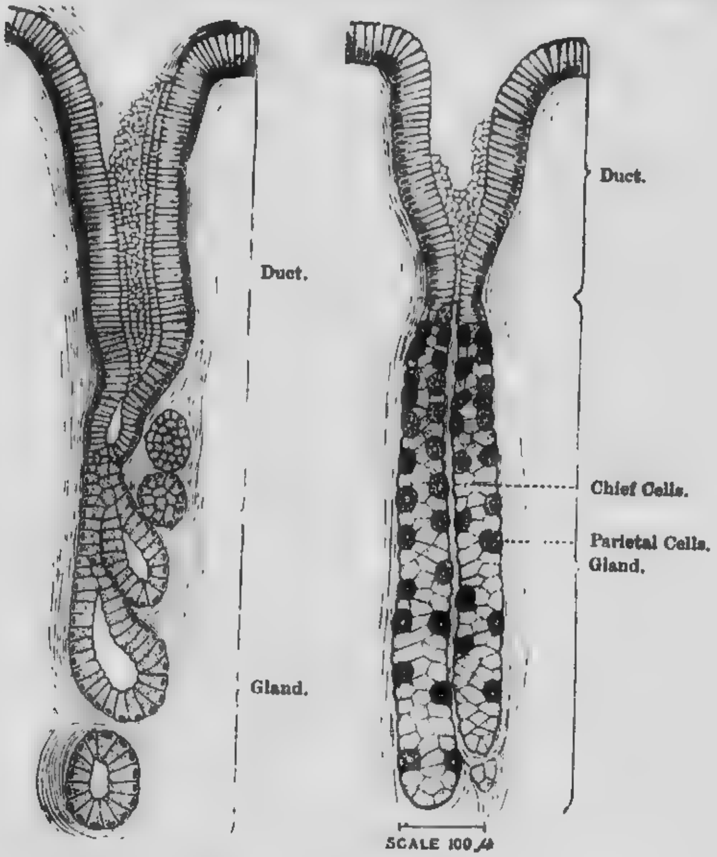
The **reaction of the contents of the stomach** is strongly acid; this acid reaction may be obtained on the cuticular as well as the villous portion of the lining, and is very persistent; the cuticular membrane even after prolonged washing gives an acid reaction. The acidity is derived entirely from the juice secreted by the villous membrane of the fundus. Our observations on this subject do not agree with those of Ellenberger, who says that during the first hour of digestion the contents of the stomach may be alkaline; acidity, he states, then commences in the fundus and extends to the cardia, though for some time the proportion of fundus acidity is three or four times greater than that of the cardia; in the course of five or six hours the proportion of acid throughout the stomach is equal. When the stomach is empty, as after a few days' starvation, its reaction is neutral or alkaline. We have observed extreme alkalinity towards the pylorus under these conditions, due no doubt to the regurgitation of bile and pancreatic fluid.

The Stomach Acids.—It is not necessary here to enter into any detail as to the nature of the gastric acids; both in the horse and man a considerable amount has been written to prove that the acidity depends upon lactic or hydrochloric acids, and it is possible that both these views may be reconciled. Ellenberger and Hofmeister are of opinion that shortly after a meal lactic acid predominates in the horse's stomach to be replaced by hydrochloric acid some four or five hours after the commencement of feeding. These observers found that the nature of the acid depended upon the region of the stomach, the period of digestion, and the character of the food; oats induced an outpouring of hydrochloric acid, whilst hay favoured the organic acids.

The following are Ellenberger's views on the nature of the stomach acids: In the contents of the stomach, hydrochloric, lactic, butyric and acetic acids may be found, the two latter in insignificant quantities only. In flesh feeders HCl predominates, ·25 per cent., and lactic acid is found, in small quantities. In vegetable feeders lactic acid at first predominates, ·4 per cent., and later HCl is present in small quantities; lactic acid exists throughout the whole stomach, but predominates in the right and left sacs, whilst hydrochloric acid principally exists in the fundus region. Lactic is the first digestive acid employed, but towards the end of a long digestion hydrochloric exists throughout the whole stomach. The amount of lactic acid found in the stomach of the horse during the first hours of digestion is considerable.

Having gone carefully into the question of the presence of hydrochloric acid and organic acids in the stomach contents, we can only say that, no matter at what period of digestion observations have been made, we have only two or three times succeeded in finding hydrochloric acid in the stomach of the horse, and are convinced that lactic is the chief, if not the sole, digestive acid in this animal.

The **Secretion of Gastric Juice** is accomplished in certain glands known as the gastric. In man these are divided into cardiac and pyloric, each having not only a different structure but a separate function. In the horse cardiac glands are impossible owing to the presence of the cuticular coat; but it has been shown that the villous coat contains glands corresponding to cardiac, which are principally situated in the greater curvature, at the fundus of the stomach, and extending over a limited area, described on p. 152 as not larger than 1 square foot (Fig. 39). The two kinds of gland employed in the production of gastric juice are both found in the villous coat, the one in the fundus, the other in the pyloric portion, though Ellenberger states that he has found fundus glands in the pyloric region. They are simple or divided tubes lying side by side, and opening, generally in groups, on the surface of the mucous membrane by means of a shallow depression in the coat. These depressions can readily be seen studded over the tunic of the fundus, giving it a rough appearance owing to the elevation of the mucous membrane between the openings of the glands; in the pyloric region the membrane is as smooth as that found in the intestine. Each



PYLORIC GLAND. CARDIAC OR FUNDUS GLAND.

FIG. 42.—THE GASTRIC GLANDS AFTER HEIDENHAIN (WALLER).

gland consists of a body, neck, and mouth, and is lined with cells; it is in respect of the cellular contents that the pyloric and fundus glands differ.

The cells of the **fundus gland** (Fig. 42) are small, polyhedral, granular, and nucleated, and line the lumen of the gland; they are called the *principal*, *central* or *chief cells*. Scattered amongst the principal cells, but existing in larger numbers at the neck of the gland than at its base, are found certain large cells (oval, granular, and nucleated), which from their position relative to the lumen of the gland are called *parietal*, *marginal*, or *border* cells. These cells are distinctive of the fundus glands, and they stain readily with aniline blue.

The **pyloric gland** (Fig. 42) below its neck has but one variety of cell—viz., the cylindrical—containing a nucleus at its attached edge. The duct is lined, above the neck, by the ordinary epithelium of the stomach, and the same remark applies to the fundus glands; it is from this epithelium that the mucus is secreted. The important distinction between the fundus gland with its principal and parietal cells, and the pyloric gland with only its principal cells, is that the former secretes both the pepsin and acid of the gastric juice (the acid being separated from the blood by the parietal cells), whilst the pepsin only is formed by the principal cells. The pyloric glands, on the contrary, only secrete pepsin and no acid.

We have previously mentioned that the cells of the salivary glands undergo certain changes in appearance, the result of rest and activity; the same remark applies to the **gastric follicles**, in which the general type of changes during secretory activity is very closely allied to those already described. Langley has found that in the active state the granules decrease in number, the cells becoming clear, and capable of differentiation into a clear outer and a granular inner zone, just as we have seen in the parotid gland; during rest the entire cell became granular. The parietal cells during digestion were found to increase in size but did not characteristically lose their granules. The central cells secrete both the pepsin and rennin ferments, but in neither case do these exist as such in the cells, but as a mother substance or *zymogen* of the ferments. The formation by the parietal cells of a free acid from the alkaline blood is a special chemical change, the result of selective powers possessed by the cells. In those animals, such as the dog, yielding hydrochloric acid, the cells very possibly form it by an inter-action of the sodium chloride and sodium dihydrogen phosphate of the blood.

Mucin is secreted by mucous glands found in the deep layers of the villous membrane, especially in the region of the fundus; the epithelial cells lining the excretory ducts of the gastric glands also take part in the process. The amount of mucin formed in the stomach of the horse is remarkable; it adheres to the villous coat like unboiled white of egg, and cannot be washed away even by a powerful jet of water. The amount secreted is unknown but must be considerable; less is formed during hunger than during activity, and there is less in ruminants than in horses.

Gastric Juice.—It is only lately that a pure sample of gastric juice (but not from the horse) has been available for analysis. Most of the previous secretions examined have been a mixture of saliva, gastric juice, and perhaps other substances. Pawlow devised a method by which the stomach of the dog could be rendered available for physiological enquiry, and a pure secretion was obtained (see Figs. 43 and 44).

Pure gastric juice in the dog is as colourless as water, thin, transparent, and of strongly acid reaction. Chemically it consists of acid and enzymes, the acidity, which is due to hydrochloric, being about ·46 or ·56 per cent. The enzymes are pepsin and rennin; the former is unable to act excepting in an acid medium, and furnishes the only example in the body of this necessary combination. How far the gastric juice of other animals resembles that of the dog in composition and appearance we do not know owing to the difficulty in obtaining it pure, but in all cases an acid and an enzyme are present. The enzyme is invariably pepsin, but the acid is not always hydrochloric. The amount of juice secreted is uncertain, in the dog some 700 c.c. (24½ ozs.) have been collected in a few hours, from which we may perhaps imagine that a considerable amount is formed in the stomach of the larger animals.

The gastric juice of the dog withstands putrefaction for a long time; it may be kept for months without undergoing any important change; not so with herbivora; the mixed gastric fluids of the horse rapidly putrefy. The antiseptic properties of the dog's juice are attributed to its hydrochloric acid; if this is so it is additional evidence against the acid of herbivora being hydrochloric. There appears to be no reason why lactic acid should not be formed by the marginal cells of the fundus glands, but an important source of lactic supply in herbivora is the carbohydrate of their food.

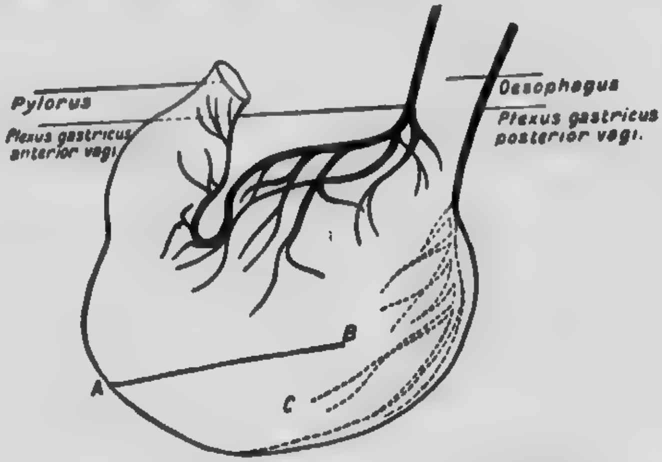

Pylorus
Plexus gastricus anterior vagi
Oesophagus
Plexus gastricus posterior vagi
B
A
C

FIG. 43.—PAWLOW'S STOMACH POUCH (STEWART).

A, *B*, line of incision; *C*, flap for forming the stomach pouch. At the base of the flap the serous and muscular coats are preserved, and only the mucous membrane divided, so that the branches of the vagus going to the pouch are not severed.

Pepsin is of a proteid nature, though very little is known of it chemically. It best exhibits its action at a temperature of the interior of the body (37° to 40° C.); a low temperature retards its activity, while it is destroyed at a high one. The ordinary commercial product is very impure; it is an extract of the mucous membrane of the stomach, to which starch or milk sugar has been added. In physiological work a glycerine extract of the mucous membrane of the stomach suffices, to which is added some dilute HCl. Glycerine has the power of extracting the ferments both from the stomach and other portions of the digestive tract such as the pancreas. The action of pepsin is almost wholly if not entirely confined to the proteid constituents of food. It converts the insoluble proteids into soluble ones not by direct transformation but by several stages. The products intermediate between proteid and peptone have received certain names suggestive of differences in their chemical nature, but as to all of this a good deal of doubt and speculation exists.

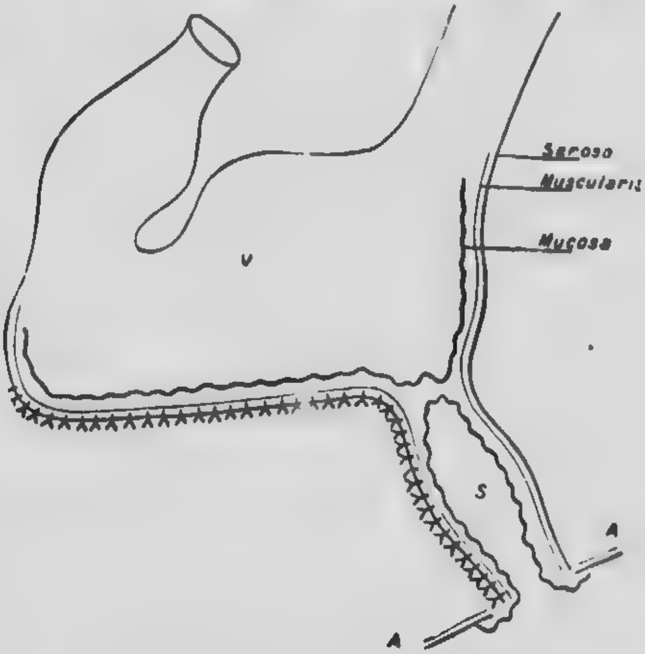
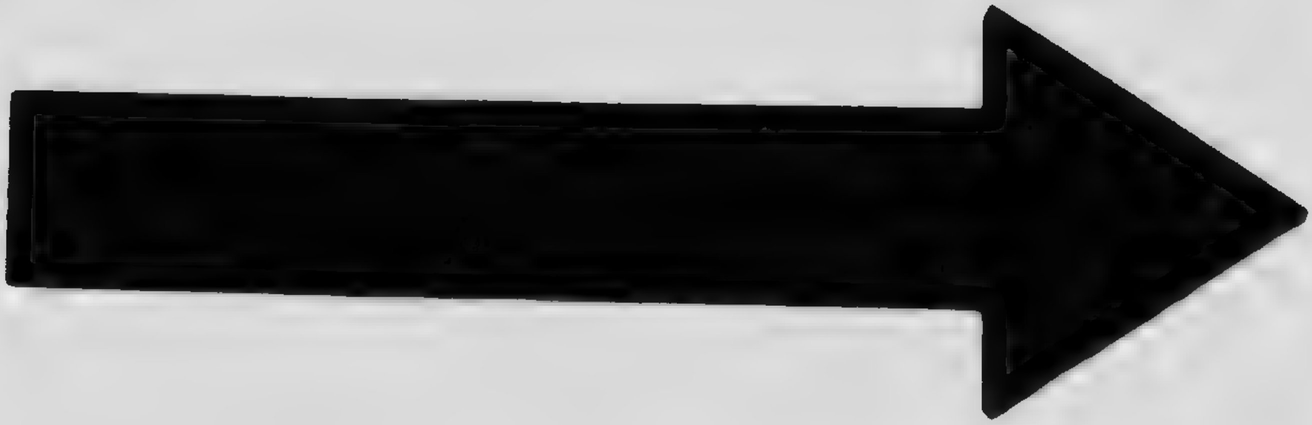


FIG. 44.—PAWLOW'S STOMACH POUCH (STEWART).

S, the completed pouch; *V*, cavity of the stomach; *A*, *A*, the abdominal wall.



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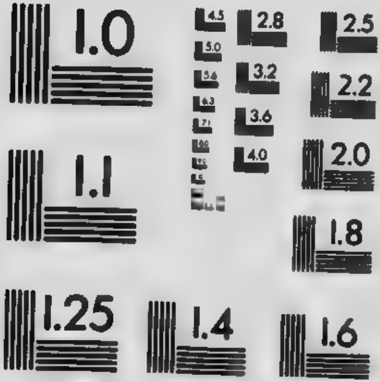

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In the following table the various stages of conversion are indicated in the order in which they are found to occur as determined by small differences in the chemical tests, such as solubility or colour reaction, yielded by the peptonized product. The table is the one drawn up by Kühne.

1. The proteid as consumed, or native albumin.
2. Acid albumin or syntonin.
3. Primary proteoses.
4. Secondary proteoses.
5. Peptones.

The proteid having reached the stage of peptones is now capable of being absorbed, but the conversion from proteid to peptone is a most complex one, during which the large proteid molecule is converted into simpler products of an infinitely smaller molecular weight, while so great is the complexity that the resulting product, peptone, is in all probability a group of compounds, rather than a single one, which only resemble each other in their solubility and their definite reaction to certain chemical tests. Rennin is the second enzyme present in the gastric juice. Commercially it is used in the manufacture of cheese, an infusion of the mucous membrane of the stomach being sufficient to produce the needful change in the milk. There appears no necessity for adult animals to possess this ferment in their juice after weaning, as milk does not form an article of diet unless we except the chemically altered milk given to the pig. In the young animal rennin plus acid causes milk to clot rapidly. The clotting under rennin resembles blood-clotting. The clot contracts after a time, squeezing out a yellowish fluid known as whey, and furthermore it is definitely known that, as in blood-clotting, a calcium salt is necessary to the process of milk-clotting. In fact two distinct steps are recognised as taking place, first the formation of a substance known as *paracasein*, by the action of rennin on casein, and secondly the action on the paracasein of the lime salts of the milk forming a curd.

If milk be deprived of its calcium salts, no clotting occurs on the addition of rennin, from which it is considered that the calcium salts are of more importance than the ferment. Rennin takes no part in the digestive process; once the curd is formed its digestion is carried out by pepsin.

Other ferment actions of the gastric juice have been described, such as fat- and starch-splitting, but of their existence there is very little evidence. Proteid digestion is the essential duty of the stomach, while in all vegetable feeders maceration of the vegetable fibres is begun in the stomach as a preliminary measure. Still in all animals a stomach is not essential to life; in the dog for example it may be removed experimentally, for as we shall see later on, proteid digestion is provided for elsewhere. But in the herbivora, especially ruminants, a stomach is essential. The chief value of the stomach in those animals which can be proved to live without it lies in the preparation of the food for subsequent digestion in the small intestines, for it is quite undoubted that proteid previously acted upon by gastric juice is far more thoroughly handled by the pancreatic fluid than proteid not so previously acted upon.

The secretion of gastric juice has but recently been proved to be under the control of the nervous system, and the secretory fibres are contained in the vagus.* Stimulation of the peripheral end of the divided nerve causes after a short delay a flow of fluid. The cause of the latent period is unknown. It can be shown in the dog that mastication, swallowing, taste, odour, etc., are direct excitants of the secretions, for they cause a copious production of gastric juice, though not if the vagus has been previously divided. If the œsophagus of a dog be divided and the upper section brought outside the wound, the animal may be indulged in a meal which never enters the stomach, but which, nevertheless, produces a profuse secretion of gastric juice. Mechanical stimulation of the mucous membranes of the stomach has no effect in producing secretion. Certain foods in the case of the dog, such as meat extracts, are most effective stimulants, while bread and white of egg are found to have no effect if introduced directly into the stomach, though they operate reflexly through mastication and taste. Finally, Pawlow, to whom all this work is due, believes that the quantity and quality of the gastric juice will be found to depend on the character of the food, so that while in some cases an economical production is arrived at, in others a stronger or weaker fluid is poured out depending upon the work to be done, the regulation of which is probably a specific action on the part of the food itself.

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* Pawlow, 'The Work of the Digestive Glands.' Translated by Thompson, 1902.

Such, briefly, is the case as it stands at present. If the above proves to be correct, we have in our hands a most likely explanation of some of the digestive troubles of the horse.

There are other changes occurring in the stomach independently of peptonizing or of gastric juice. If a horse be fed on oats and the stomach fluid examined, it will be found to contain an abundance of sugar. The sugar is produced from the starch of the grain, and is not, according to our observations, the result of the action of saliva. Abundant saliva exists in the stomach, but it will be remembered that in the horse we have never succeeded in getting it to give any evidence of starch conversion. The question, therefore, is, What is the cause of this formation of sugar? It has been shown that oats may yield a starch-converting ferment, and the view that the grain provides its own enzyme for the conversion of starch into sugar may be provisionally accepted as the explanation of the presence of sugar in the stomach of the horse. The whole of the starch is not thus converted, for distinct evidence of unaltered starch can be obtained in the first portion of the small intestines. Further, some of the starch is no doub converted into lactic acid, and the presence of this acid in the proportion of 2 per cent. does not in any way inhibit the amylotic action. If oats provide their own starch-converting enzyme, we see the strongest argument against boiled food for horses, a practice we believe to be deleterious or even dangerous.

Fats are not acted upon in the stomach, though the envelope surrounding the fat globule is digested, and the fat set free.

Cellulose fermentation is considered by Tappeiner to occur in the left sac of the stomach, and when marsh-gas has been found in this organ, it results from cellulose decomposition. Brown* has shown that the destruction of the cell-wall of oats and barley occurs in the stomach, where it is dissolved by a cyto-hydrolytic ferment *pre-existent in the grain;* the changes occur with extraordinary rapidity in the stomach of the horse. The researches of this observer on a cellulose-dissolving ferment are of the greatest interest to the veterinary physiologist, and of considerable practical importance.

Periods of Stomach Digestion.—Stomach digestion in the horse has been divided by Ellenberger and Hofmeister into certain periods corresponding to definite chemical changes in the food. For example, it is said that during the two first periods, which between them last two and three hours, starch conversion, lactic acid fermentation, and proteid conversion to a limited extent occur. In the third period mixed digestion of starch and proteid occurs, while in the fourth and last period only proteid digestion takes place. The third and fourth periods may together last four hours and upwards. We must be careful to avoid regarding these periods as based on some rigid law; they are very variable in duration, due to causes we have previously considered, and run imperceptibly into each other. With this caution we give the following periods at which gastric digestion is said by Ellenberger and Hofmeister to be at its maximum in the horse:

After a moderate feed digestion is at its height in 3 or 4 hours.
„ full „ „ „ „ 6 to 8 „
„ an immoderate „ „ delayed still longer.

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* 'On the Search for a Cellulose-dissolving Enzyme,' H. J. Brown, F.R.S., *Journal of the Chemical Society*, 1892, p. 352.

Stomach Digestion in Ruminants.—The **Rumen** or first gastric reservoir is a viscus of enormous proportions, capable in the ox of holding 60 gallons. It is divided into four sacs by means of very thick muscular pillars, and the whole is lined by a well developed mucous membrane, in part covered by leaf-like papillæ. The mucous membrane, it is said, contains some small glands which are not considered to provide any digestive secretion. The rumen is in connection with the reticulum, and by means of the œsophageal groove with the omasum. All solid food on first coming from the mouth is received by the rumen and, judging by the contents of this compartment, much of the fluid which is swallowed must also find its way there; it has been proved by the experiments of Flourens that fluid may find its way from the œsophagus into all four stomachs at one and the same time. The amount of fluid in the rumen is important from a digestive point of view, since rumination is impossible unless a large proportion of water exists in this cavity. The fluid found in the rumen consists of the water which has been consumed, of the amount of saliva swallowed, and of the amount existing in the food; but much of it is saliva, of which the ox secretes enormous quantities.

The contents of the rumen are alkaline, which is probably owing to the saliva; in appearance they resemble food which has been coarsely ground. This mass is slowly and deliberately, not energetically, revolved within the stomach, the material at the posterior part being gradually forced upwards and forwards and so a complete mixing occurs. The churning movement is brought about by the extremely powerful muscular pillars of the organ, which are so arranged as to separate it into various sacs; these pillars, when they contract, shorten the rumen in its two diameters, and press the contents towards the opening of the œsophagus. Fermentation may also assist to mix the contents, owing to the evolution of gas during the process. It is due to the churning movement that the 'hair balls,' found in the rumen of cattle, are formed.

The essential function of the rumen is to retain the food for remastication, to macerate all fibrous substances and to fit them for cellulose digestion, which here takes place possibly under the influence of ferments contained in the food itself. The amount of cellulose digested in the rumen has been estimated at between 60 and 70 per cent. Ellenberger is of opinion that in addition to the functions named, other digestive changes occur; he says that carbohydrates are digested by means of enzymes contained in the food, and in this way starch and cane sugar are converted into maltose. Proteids are also slowly converted into peptones, not through any true peptic ferment but by some enzyme provided by the food. The result of the decomposition of cellulose is the production of a considerable quantity of gas. The rumen never empties itself; even after prolonged starvation it contains food. In young ruminants digestion occurs principally in the fourth stomach, the other compartments being rudimentary; when the young animal is placed on solid food it is remarkable how soon these compartments develop, and the process of remastication is established.

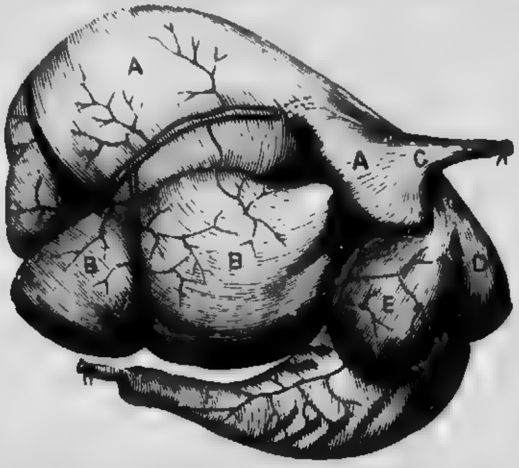

Fig. 45.—The Gastric Compartments and True Stomach of Ruminants (Colin).

C, The œsophagus; A, A, B, B, the rumen; D, the reticulum; E, the omasum; F, the abomasum.

The **Reticulum** or second gastric reservoir is a small one. Its interior is arranged like a honeycomb, in the cells of which foreign bodies such as stones, sand, nails, etc., may be found. The contents of this compartment are fluid and alkaline, the fluid being derived from that swallowed, and from the rumen; the alkaline reaction is due to the saliva, for so far as we know, the mucous membrane possesses no secretory activity. The fluid in the reticulum is of use in rumination, and is forced into the œsophagus by a contraction of the walls of the viscus; in order that fluid may be retained in this compartment the openings out of it are situated considerably above the base of the organ, and further, the reticulum is so situated relatively to the rumen that it receives the overflow of fluid from that compartment when it contracts.

Ellenberger is of opinion that the reticulum regulates the passage of food from the first to the third compartment, and from the rumen to the œsophagus. In transferring the contents of the rumen to the omasum, the reticulum contracts and forces the material into the open œsophageal groove. That the reticulum is capable of energetic contraction is specially noted by Colin, whose observations on the physiology of the stomach in ruminants were mainly carried out by means of an opening in the abdominal wall. Flourens showed that the reticulum was not essential to rumination, for he excised it in a sheep and rumination was not interfered with.

The **Omasum**, or third compartment, is peculiar; its physiology has been elaborately worked out by Ellenberger. This authority says that it possesses no secreting power; that its function is to compress and triturate the food which it crushes between its powerful muscular leaves, rasping the ingesta down by means of its papillæ. The contents of this sac are always dry, due to the fluid portion being squeezed off and flowing into the fourth stomach by the action of gravity, through a passage formed in the lesser curvature of the organ. The food may find its way into the omasum, either directly from the œsophagus after remastication, or from the first or second compartments. It is probable that its chief source of supply is directly from the œsophagus, the omasum being drawn forwards towards it by a contraction of the pillars of the œsophageal groove, by which means communication with the rumen and reticulum is cut off. Normally the reaction of the contents of the omasum is neutral; if found acid it is due to regurgitation from the true stomach. It is peculiar in possessing a separate source of nerve supply, stimulation of the pneumogastric producing contraction of all the other compartments but this.

The **Abomasum** is the true digestive stomach, and is the only compartment secreting gastric juice. In the abomasum proteids are converted into peptones, the region of the cardia being in this respect more active than the pylorus. Ellenberger states that starch is also digested, and that this precedes proteid digestion. In the fourth stomach of the calf a milk-curdling ferment (rennin) exists, which has already been dealt with.

Stomach Digestion in the Pig.—The stomach of the pig is peculiar; it is a type between the carnivorous and ruminant, and is divided by Ellenberger and Hofmeister into five distinct regions, which do not all possess the same digestive activity.

The gastric juice of the pig contains for the first hour or two of digestion lactic, and afterwards hydrochloric acid; pepsin is present, and, it is said, a ferment which converts starch into sugar. In the pig, according to the above observers, the process of digestion is not the same in all regions of the viscus; one may contain hydrochloric acid, another lactic; one may be abundant in sugar, while this may be absent elsewhere. The first stage of digestion is one of starch conversion; the second stage is the same only more pronounced; the third is one of starch and proteid conversion, both processes occurring at the cardia, but only proteid conversion taking place at the fundus; lactic acid is present in the former and both lactic and hydrochloric acid in the latter. In the fourth stage starch conversion is nearly complete, hydrochloric acid predominates in all the regions, and proteid conversion is general.

Stomach Digestion in the Dog.—Very complete knowledge of the physiology of the dog's stomach exists, for nearly all the work carried out to elucidate the physiology of the human stomach has been effected on the dog, and has, more or less, been already embodied in the previous pages in dealing with gastric juice.

A flesh diet requires very little saliva and practically no mastication, but its digestion is slow, in spite of the fact that it is taken in a form closely allied to that in which it is assimilated. Colin states that it takes a dog twelve hours to digest an amount of meat which it could eat at one meal. The substances most difficult of digestion are tendons and ligaments, but their digestion is facilitated by boiling; liver and flesh are best given raw as cooking interferes with their digestibility. The gastric juice of the dog contains pepsin and hydrochloric acid ·46 to ·56 per cent., and it has been shown that it is possessed of considerable activity, and certain peculiarities which have been dealt with on p. 165.

Absorption from the Stomach.—The needful changes having occurred in the stomach—and we now refer principally to the stomach of the horse—the next step is to inquire into the proportion of food so altered as to be rendered fit for absorption.

Experiment shows that in the stomach 40 to 50 per cent. of the carbo-hydrates have been converted into sugar, whilst 40 to 70 per cent. of the proteids are converted into peptones; when food has been long in the stomach, not more than 10 per cent. of the proteids escape being peptonized. In ruminants probably the greater part of the food substance is acted upon in the gastric compartments and stomach, leaving comparatively little for the intestines to perform.

In spite of the changes which occur in the stomach, it has been proved by the experiments of Colin that *no absorption occurs from this organ in the horse.* It would be useless to recapitulate all his experiments; they were generally performed with strychnine, and he found, that so long as the pylorus was securely tied, no symptoms of poisoning occurred when the alkaloid was introduced into the stomach, no matter how long it was left there, but that when the ligature was untied, and the contents of the stomach passed into the intestines, poisoning rapidly followed. These remarkable results were obtained by him so often, and under such varying conditions, as to leave no doubt as to the accuracy of the observations. Strychnine experiments are not altogether free from objection, but as matters stand we can only surmise that no absorption of sugar or peptones occurs in the stomach. It is certainly very remarkable what becomes of the peptones; we have never found any in the stomach contents, no matter at what period of digestion the examination was made, and if they are not absorbed in the stomach they must pass very rapidly into the intestines and enter the vessels at once, as no peptone can be found in the small intestines. Colin attributes the absence of absorption from the stomach of the horse to the small area of the mucous membrane, which, he says, cannot be secreting gastric juice and absorbing at the same time. In the empty stomach he attributes the non-absorption of poisons to the thick layer of tenacious mucus which, as we have previously mentioned, covers the villous stomach of the horse. Colin's experiments also show that there is little or no absorption from the abomasum of ruminants. On the other hand, there is absorption from the stomach of the dog and pig. Recent experiments on the dog show that absorption does not take place readily from the stomach. Water taken alone is practically not absorbed at all; sugars and peptones are absorbed only when in sufficient concentration, while fats are not absorbed.

Self-digestion of the Stomach.—A question which for a long time gave rise to an energetic discussion, was the reason why the stomach during life does not digest itself, seeing that the action of its secretion is so potent that portions of living material, legs of frogs, ears of rabbits, etc., if introduced into it are readily digested, also that post-mortem digestion of the stomach in some animals is far from rare. It is believed that the gastric epithelium forms an antibody, known as antipepsin, which neutralizes the digestive action on the living wall. This view is the outcome of recent studies in immunity (see p. 26). We have never yet met with post-mortem digestion of the stomach in the horse; whether this be due to the horse's acid being mainly or wholly lactic cannot be definitely stated.

The Gases of the Stomach.—The nature of these largely depends upon the food—for example, green food is most productive of gas owing to the active fermentation it undergoes. Traces of oxygen, a quantity of carbonic acid, and variable amounts of marsh-gas, sulphuretted hydrogen, hydrogen, and nitrogen are found. The oxygen and nitrogen are derived from the swallowed air, the carbonic acid is derived from the fermentation of the food, and the action of acids on the saliva, whilst the marsh-gas is obtained by the decomposition of cellulose.

The gases from the intestines of the horse and rumen of the ox are very commonly inflammable, and burn with a pale blue flame. This is due to marsh-gas, which may be readily ignited when mixed with a due proportion of oxygen.

Vomiting.—Vomiting amongst solipeds and ruminants is rare, but the act is common in the dog and pig.

The reasons given as to why the horse does not *ordinarily* vomit are various: (1) the thickened and contracted cardiac extremity of the œsophagus; (2) the oblique manner in which the latter enters the gastric walls; (3) the dilated pylorus lying close to the contracted cardia, so that compression of the stomach contents forces them into the duodenum; (4) the cuticular coat thrown into folds over the opening of the cardia; (5) muscular loops encircling the cardia, the contraction of which keeps the opening tightly closed; (6) the stomach not being in contact with the abdominal wall.

All these and other reasons have been assigned as the cause of non-vomiting in the horse. Yet on turning to ruminants, which also normally do not vomit, we find the stomach, gastric compartments, and œsophagus freely communicating; the largest reservoir lies in contact with the abdominal wall, the cardia is freely open, the œsophagus is of great size, and, still stranger, the animal possesses the ability, under the control of the will, to bring up food from the stomach as a normal condition, and yet cannot vomit! It is evident, therefore, that all these theories are not sufficiently satisfactory to account for the absence of vomiting, and we are bound to suppose that the vomiting centres in the medulla of both horse and ox are either only rudimentary or very insensitive to ordinary impressions.

Vomition in the horse is no doubt seriously interfered with by the thickened œsophagus, contracted cardia, and the arrangement of the muscular fibres. The folds of mucous membrane filling up the orifice could offer no serious obstruction to a distended stomach, for we know that even when this membrane is dissected away post-mortem, a stomach will burst rather than allow fluid or air pumped in at the pylorus to escape at the cardia, unless the muscular fibres surrounding it be partly divided. Vomition in the horse is generally indicative of ruptured stomach, and much has been written as to whether vomiting occurs before or after rupture. From no inconsiderable experience of these cases, we have arrived at the conclusion that it may occur at either time, and that a horse may vomit though a rent seven or eight inches long exists in the stomach wall.

Dilatation of the cardia and œsophagus is essential to the act of vomition in the horse, and in all cases where vomiting occurs during life, the cardia is so dilated that two or three fingers may readily be introduced into it. It is perfectly possible for a horse to vomit and recover (showing that it had not a ruptured stomach), and it is not unusual to have attempts at or actual vomition when the small or large intestines are twisted. Vomiting in the horse is not as a rule attended by any distressing symptoms; the ingesta dribble away from one or both nostrils; occasionally an effort is made on the part of the patient, the head being depressed to facilitate expulsion, but more than this is very rarely seen.*

It is important to notice in connection with the subject of vomiting that agents such as tartar emetic, ipecacuanha, and apomorphia, which excite vomiting by their action on the cerebral centre, have no effect on the horse or ruminants, nor does the horse vomit as the result of sea-sickness, though he suffers extremely from it. Why he should vomit more often with a ruptured stomach than a sound one is a fact we cannot explain.

In those animals where vomiting is a natural process, the three important factors are, the dilatation of the cardia by active contraction of the longitudinal fibres of the œsophagus, pressure on the walls of the stomach by a contraction of the diaphragm and abdominal muscles, and closure of the pylorus. But there is some evidence to show that the stomach itself is not passive; it is true Majendie produced vomiting after he had replaced the stomach by a bladder, but under normal conditions there appears no reason why the stomach wall should remain quiescent, and in the cat it has been observed that during vomiting a strong contraction of the pyloric end of the stomach occurred, shutting it off from the cardiac portion. We may here have one explanation of ruptured stomach in the horse.

Rumination.

The physiology of rumination has been principally worked out in France by Flourens and Colin, and our knowledge of this singular process is based almost entirely on their observations. *Œsophageal Groove.*—The œsophagus in ruminants enters and passes through the rumen, forming a singular groove or channel known as the œsophageal, which on the left communicates with the first and second compartments, and by an opening on the right and inferiorly, with the third compartment (Figs. 46 and 47). In this way food coming down the œsophagus may enter either of the first three reservoirs, the choice being determined, as we shall presently point out, by the condition in which it is swallowed.

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* The only case of vomiting we have seen in the horse which resembled that presented by the human subject was in a case of volvulus of the small bowels. The horse was lying on his chest with the nose extended, the ingesta gushed in a stream from both nostrils, and a sound accompanied the effort.

The œsophageal groove possesses two lips or pillars, the anterior being formed by the reticulum, the posterior by the rumen. The lips are thin above, and thick below where they overlap; normally they lie in apposition in such a way as to conceal the groove, but in both Figs. 46 and 47 they are intentionally separated in order to show the arrangement. These pillars are composed of involuntary muscular fibres arranged longitudinally and transversely, by which means the groove can be shortened and constricted. By a contraction of the pillars the omasum may

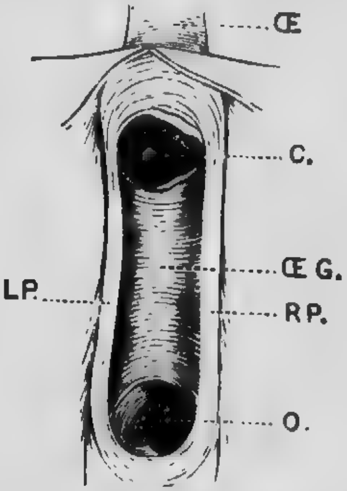

Fig. 46.—Diagram of the Œsophageal Groove (Carpenter).

œ, Œsophagus entering the stomach; c, its cardiac opening; rp, right pillar of œsophageal groove; lp, left pillar of the same; o, opening into the omasum; œg, œsophageal groove extending from c to o, about 7 inches in length. To the right of the figure is the rumen, to the left the reticulum.

be shut off from the first and second compartments, and brought nearly in apposition with the œsophagus; or by their relaxation the first and second may be made to communicate with the third compartment. When the pillars are relaxed the œsophagus communicates more directly with the rumen and reticulum. Another function of the groove was said to be to cut off a pellet of food pressed into it by a contraction of the rumen and reticulum, the pellet or bolus

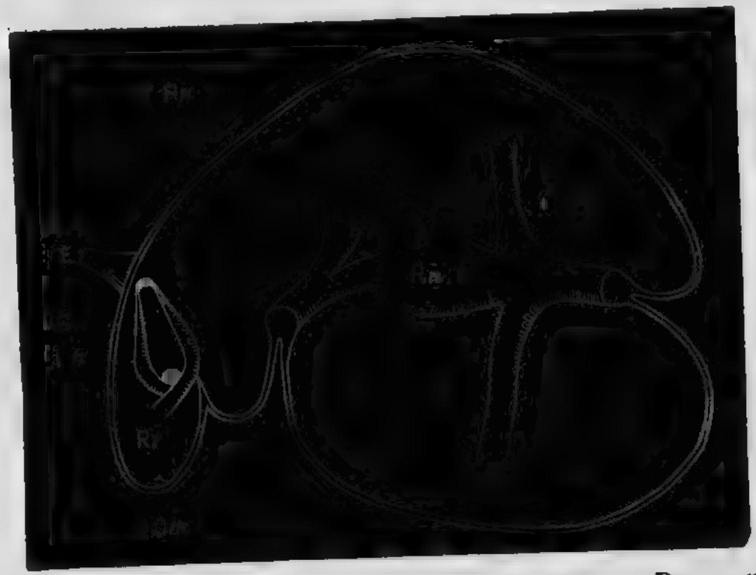

Fig. 47.—Longitudinal Section of the Rumen and Reticulum to show the Position of the Œsophageal Groove in the Living Animal.

Ru, rumen; the lettering is placed on the muscular pillars, which are held apart. *Rt*, reticulum. Œ, œsophagus. *Rp*, right pillar; *Lp*, left pillar: both held widely apart to show G, the groove. *Om*, opening leading to the omasum.

being then passed into the œsophagus for remastication. Colin has shown that if the lips of the canal be stitched together rumination may still occur, so the theory that the bolus is formed between these lips is not correct, and this view is supported by the stomach of the llama, which only possesses one pillar.

Colin's description of the mechanism of rumination is as follows. During the churning movement the food is gently pressed against the lips of the groove, when, by a spasmodic contraction of the diaphragm and abdominal muscles, some of the liquid from the reticulum and some of the solid from the rumen is carried up the œsophagus, while the latter, by the contraction of its funnel-shaped extremity, cuts off the bolus, and by its reversed peristaltic action conveys it to the mouth. In passing under the velum palati the liquid portion is squeezed out and is at once reswallowed, travelling to the third compartment, while the solid mass undergoes grinding. After the bolus is reswallowed it may either return to the rumen, or, if in a finely comminuted condition, it passes at once from the œsophagus into the third compartment. The reticulum appears to be only a convenient accessory to rumination, for, as previously mentioned, Flourens excised it without interfering with the process of rumination. During the process of rumination the parotid glands secrete, but not the submaxillary or sublingual.

Rumination is a reflex nervous act, the centre for which probably lies in the medulla. The process can only be performed by means of the united action of the diaphragm, walls of the stomach and abdominal muscles. Hence, if the phrenics be divided rumination is carried out with great difficulty, and only by an extra effort of the abdominal muscles; if the vagi be divided the walls of the stomach are paralyzed and the process cannot go on; if the spinal cord be divided in the mid-dorsal region the abdominal walls are paralysed and rumination can no longer occur. The condition of the stomach and its contents also exercises an important influence; rumination can only take place when the organ contains a fair amount of food and a considerable quantity of liquid. The ascent of the food in the œsophagus can be distinctly seen in the neck, and sounds may be heard on auscultation due to the passage of the bolus with its fluid admixture, and the friction of the rumen against the diaphragm. The amount of each bolus has been estimated by Colin at 3½ to 4 ozs.;

its formation in the stomach and ascent occupies about three seconds, and its descent after remastication one and a half seconds: its remastication occupies about fifty seconds. On these data Colin has calculated that at least seven hours out of the twenty-four are required for the process of rumination.

Movements of the Stomach begin very shortly after food is received. Waves of peristalsis travel from the middle of the organ towards the pylorus; these waves become stronger as digestion proceeds, and their function is to press the peptonized food against the pylorus. The pylorus is kept tightly closed, and only relaxes to allow a stream of chyme to be ejected, which occurs with considerable force. The left or œsophageal end of the stomach in all animals plays but a passive part, and may be regarded in animals with a single stomach more in the light of an œsophageal dilatation, a characteristic particularly indicated in the horse. There is very little movement in the left end of the stomach, and this permits starch conversion to go on undisturbed, especially in the last portions of food swallowed.

It is probable that in all animals with a single stomach churning movements are unnecessary, and it is certain they do not occur in the horse, for in feeding on three or four different foods they are all found arranged in strata in the stomach, in the order of their arrival. In ruminants, on the other hand, other movements are clearly indicated: the immense muscular pillars of the rumen are capable of rotating the contents, and the formation of balls in the rumen, from hair swallowed when licking the body, is most suggestive of rotatory movement. Eber of Dresden says that in the ox the rumen normally contracts a little more than three times in two minutes.

The relaxation of the pylorus is a distinct mechanism: it only occurs when material is ready to pass out, and not with every contraction wave which passes over the organ. Yet this statement must be modified in the case of the horse, where, as we have shown, owing to the small size of the stomach, and the bulky nature of the food, an amount passes out at the pylorus equal to that received at the cardia. Liquid foods readily pass the pylorus, and probably most liquids pass rapidly out of the stomach. It is especially so in the horse, in which animal the water as consumed sweeps directly through the stomach, and may, on auscultation, be heard passing along the duodenum to the large intestines.

The movements of the stomach are excited by the presence of food, or any irritation applied to the mucous membrane. These movements are rendered more energetic by stimulation of the vagus, but even when all the nerves going to the part are divided, the stomach can still contract, which is probably due to the ganglia contained in its walls. The stomach is in fact an automatic organ. Both pneumogastrics supply the stomach, the nerves being non-medullated. In addition it obtains sympathetic fibres from the solar plexus, to which the right vagus also sends some fibres (see Fig. 55, p. 206). In the wall of the stomach are found ganglia with which both the vagus and sympathetic communicate. The vagus may be regarded as the motor nerve of the stomach, while the sympathetic is mainly inhibitory; stimulation of the vagus leads to contraction of the stomach walls, stimulation of the sympathetic causes dilatation of a contracted stomach and relaxation of the pylorus. The vagus supplies the bloodvessels with dilator fibres, whilst the sympathetic supplies them with constrictor fibres. Section of the vagus in the horse causes paralysis of the stomach and in other animals; if the movements are not abolished, they are certainly diminished. The result of stomach paralysis is that nothing passes on to the intestines, so that in the horse even large poisonous doses of strychnia may thus fail to cause death by lying inert in the stomach. This experiment demonstrates the uselessness of giving medicine by the mouth in many cases of digestive trouble in the horse; the material lies in the stomach owing to paralysis of the organ, and is never absorbed. The secretory nerves of the gastric glands have been dealt with on p. 169.

The *nervous mechanism of the stomach of ruminants* is derived mainly from the vagus, excepting for the third compartment, which has a separate and, at present, unknown source of supply. Stimulation of the vagus was found by Ellenberger to produce energetic contraction of the reticulum, slow kneading movements of the rumen, and slower and later-appearing peristaltic contractions of the abomasum, but no contraction of the omasum. Section of both vagi was found to paralyse the œsophagus, rumen, and reticulum, followed by tympany of the rumen. Ellenberger could not obtain any effect on the stomach movements by stimulating the sympathetics.

SECTION 3.

Intestinal Digestion.

The chyme which is poured from the stomach into the small intestines meets there with three digestive fluids, viz., the succus entericus, the bile, and the pancreatic juice.

The **Succus Entericus** is prepared by the glands of the small intestines; in the duodenum the glands of Brunner are found, whilst the follicles of Lieberkühn are met with throughout the whole of the small and large intestines. Lieberkühn's crypts supply a considerable proportion of intestinal juice, while the secretion from the glands of Brunner is scanty. Brunner's glands, which are very large in the horse, are arranged on the same principle as the gastric glands, while those of Lieberkühn are tubular glands, amongst the cylindrical epithelial cells of which numerous mucus-forming goblet cells may be found.

At one time it was considered that the succus entericus was a comparatively unimportant fluid, the chief function of which was to neutralise the acid chyme; Colin, however, showed that in the horse it had a distinctly digestive effect. It is now known that though a pure secretion of Lieberkühn's crypts has little or no digestive action excepting on starch, an extract of, and juice squeezed from the intestinal wall has a most important function. The Lieberkühn fluid is quantitatively small in amount, and alkaline in reaction due to carbonate of soda. The intestinal extract, on the other hand, contains three enzymes, and in addition a peculiar chemical substance of remarkable properties. The enzymes are :

1. *Enterokinase*, which converts the trypsinogen, the mother substance of the pancreatic proteolytic enzyme, into trypsin.

2. *Erepsin*, also a proteolytic ferment, which supplements the work of trypsin, acting on deutero-albumoses and peptones, breaking them up into amido-acids and hexone bases.

3. *Inverting ferments*, converting double sugars which cannot be utilized by the tissues into single sugars which can. Of inverting ferments there are three :

Maltase, converting maltose and dextrin into dextrose.

Invertase, converting cane-sugar into dextrose and levulose.

Lactase, converting milk-sugar into dextrose and galactose.

Finally, the intestinal fluid contains *secretin*, which is not a ferment but a chemical substance found in the walls the small intestines; this when taken into the bloo possesses the singular property of causing the secretion of pancreatic juice.

Enterokinase and secretin will be dealt with in our consideration of the pancreas.

Intestinal Digestion in the Horse.—The contents of the stomach are neutralised by the pancreatic and biliary secretions immediately or shortly after they leave the stomach. So much is this the case that on the duodenal side of the pylorus the reaction of previously acid chyme is neutral, and a few inches along the duodenum it is alkaline, this alkaline reaction is at first faint, but becomes more marked as the ileum is approached. Ellenberger describes the contents of the small intestines as being acid in the first two-thirds of their length, then neutral as far as the ileum, where they become alkaline; we have only once found them otherwise than alkaline throughout. He further states that in the fasting horse the contents are alkaline, but that in the digesting animal, whether horse, ox, or sheep, they are acid, the acidity decreasing after passing the common duct, and becoming decidedly alkaline at the posterior portion of the small intestine. This, as we have said, does not agree with our experience in the horse; it is usual to find the contents of the duodenum next the pylorus neutral, and from this point the bowel is faintly alkaline, the reaction increasing in intensity up to the ileum, where the contents are always markedly alkaline. We have only once found the small bowels acid in the horse, no matter what diet has been given, or at what period of digestion the examination has been made; a neutral or faintly alkaline reaction in the anterior part of their course, and marked alkalinity in the posterior portion, is doubtless the rule rather than the exception.

The arrangement of the small intestines suspended or dangling in festoons from the spine through the medium of a very delicate membrane is a construction the advantages of which are not very apparent. It appears to invite trouble. The long mesentery is considered to favour volvulus, but no doubt the chief cause of this latter trouble is tympany. If the bowels be artificially distended with air, loops of them behave in such a way as would lead to twist in the living animal.

Physical Characters of the Chyme.—The chyme having passed into the bowel its appearance at once changes, for the acid albumin is precipitated by the alkaline secretion found there. It is now observed that the material consists of clots floating or suspended in a yellowish fluid, extremely slimy in nature, and resembling in appearance, through its precipitated albumin, nasal mucus suspended in fluid. The proportion of mucin must be considerable judging from its ropiness when poured from one vessel to another, and this mucus is probably largely derived from the stomach.

Throughout the small intestines the character of the chyme is as follows, viz., a yellow, frothy, precipitated, slimy fluid, the material from the anterior part of the intestinal canal having a peculiar mawkish smell, whilst that from the region of the ileum is of a distinctly fæcal odour; the latter is due to indol and skatol formed putrefactively during pancreatic digestion. In the ileum the proportion of fluid material is considerably reduced in amount, and the character of the ingesta may now be recognised, which was previously almost impossible.

Function of the Ileum.—As the flow of material into the small intestines is controlled by a sphincter, so is the flow out of it. The ileum is a remarkably thick and powerful bowel, it is always found contracted and containing material which is dry compared with that found in the anterior portion of the intestine. One of the functions of the ileum is to control the passage of material into the cæcum. Colin describes the chyme in the horse as circulating between the pylorus and ileum, viz., that it is poured backwards and forwards in order to expose it sufficiently to the absorbent surface; this necessitates a reversed peristaltic action. He says that were it not for this the material could not be acted upon and absorbed, as the passage of fluid through the small intestines is very rapid. It would have been impossible to reason out that the fluid material of the small intestines was passed to and fro between the stomach and the ileum, exposed, as Colin expresses it, twenty times over to the absorbent surface of the bowels. This observation must have been made as the result of his examination of the living animal, and there can be no doubt of its correctness.

Experiment shows that water will pass from the stomach to the cæcum in from five to fifteen minutes. By applying the ear over the duodenum, as it passes under the last rib on the right side, the water which a horse at that moment is drinking may be heard rushing through the intestines on its way to the cæcum. One is always struck by the fact that the small intestines are never seen full, in fact, are often practically empty, from which we judge either that material passes very rapidly through them, or that only small amounts of chyme are propelled into them at a time. The contents are always in a liquid condition excepting at the ileum, the fluid being derived from the secretions poured into and those originating in the bowel. That active absorption goes on in the intestines is proved by the difference in the physical characters of the contents in their several parts. The rate at which the chyme passes through the small intestines varies with the nature of the food, and the frequency with which the horse is fed. Ellenberger says it reaches the cæcum six hours after feeding, but has not entirely passed into this bowel for twelve or even twenty hours; we have known it reach the cæcum in four hours.

In the small intestines the chyme meets with the bile and pancreatic juice; the action of these on food is described in the chapter dealing with the liver and pancreas. The absorption of chyle, and its elaboration before reaching the blood, are points which must be reserved for the chapter on 'Absorption.'

Large Intestines.—There can be no doubt that in solipeds digestion in the large intestines is a very important process, at least, we judge so from the fact of their enormous development. In many respects they present a considerable contrast to the small intestines; for instance, they are always found filled with ingesta, the contents are more solid, the material lies a considerable time in them, and there are no juices other than the succus entericus poured into the bowel. These are conditions exactly the reverse of those found in the small intestines. The bowels which are spoken of as the large intestines are the cæcum, double and single colon, and the rectum.

The **Cæcum** has been described by Ellenberger as a second stomach; its enormous capacity and fantastic shape have always rendered it an intestine of considerable interest (Fig. 48). To our mind its most remarkable feature is that it is a bag the openings into and out of which are both found at the upper part close together; the exit, strange to say, is above the inlet, and the contents have to work against gravity in order to obtain an entry into the next intestine, the double colon. This is brought about by the four muscular bands on the cæcum (Fig. 49), which shorten the bowel, forcing the contents upwards towards the 'crook.' The ileum being closed, the only available outlet is into the colon (Fig. 48).

Several questions suggest themselves regarding the communication between the large and small intestines. It is certain that in order to get from the ileum into the colon everything must pass into or, at any rate, through the cæcum, yet we are assured that material does not remain there long. Could it be possible for the opening of the ileum and that of the colon to be so brought together that material might pass direct from one into the other? (Fig. 50.) Nothing is returned into the ileum from the cæcum; there must be, in consequence, a sphincter keeping the ileum closed, for when the cæcum contracts

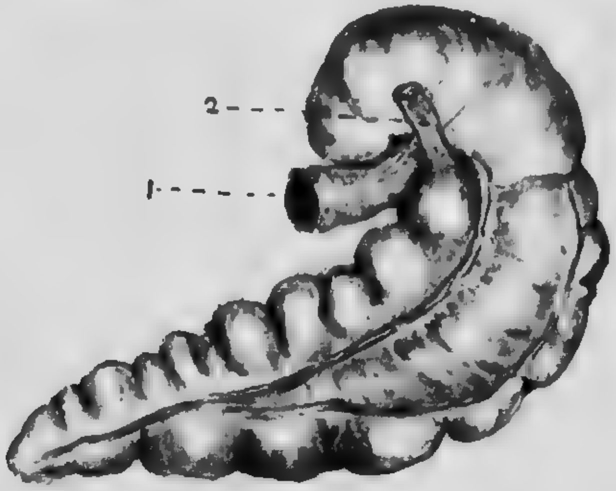

FIG. 48.—CÆCUM OF THE HORSE IN POSITION, ITS INNER FACE BEING SEEN.

1, The first colon; 2, the ileum.

material must cross the opening of the ileum in order to reach the colon. This sphincter is furnished by the thickened condition of the wall of the ileum. We see no difficulty in believing that the rigid end of this tube may pass its contents practically direct into the colon, and the slightly funnel-shaped arrangement of the latter would readily admit the rigid nozzle of the ileum.

The contents of the cæcum are always fluid, sometimes quite watery, occasionally of the colour and consistence of pea-soup, in which condition they are full of gas

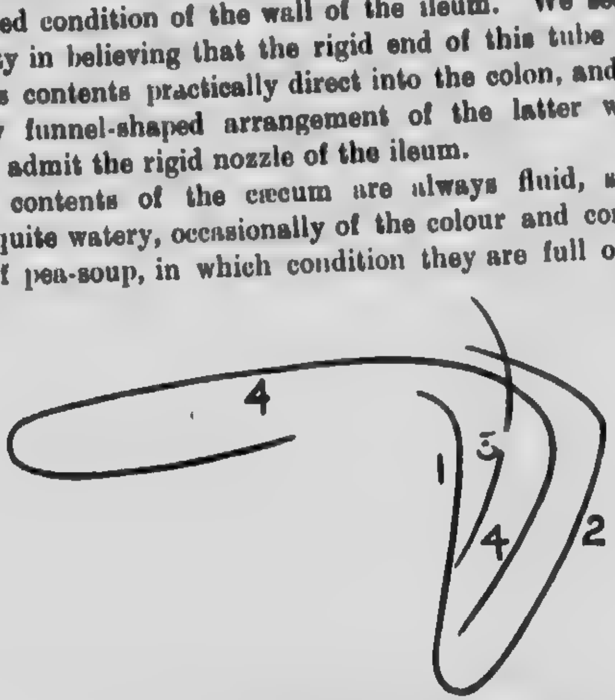

Fig. 49.—Schematic Arrangement of the Longitudinal Muscular Bands of the Cæcum.

Bands 1 and 2 are one, and form a complete sling for the bowel; band 4 runs from the cæcum to the pelvic flexure of the colon It is a remarkable band, and doubtless intimately connected with the mechanism which brings about the passage of material from cæcum to colon.

bubbles; when watery the fluid is generally brownish in colour, with particles of ingesta floating about in it. The reaction of the contents is always alkaline; all observers are agreed on this point.*

The cæcum is most admirably arranged as a receptacle for fluids, and though absorption undoubtedly occurs from it, and digestion of cellulose takes place in it, yet we believe its chief function is the storing up of water for the wants of the body and the digestive requirements, as it is absolutely certain that digestion in the horse can only be properly carried out when the contents are kept in a fairly fluid condition. We do not say that the cæcum produces no digestive changes in the food, for we have stated that the contents are occasionally of the consistence of pea-soup, but we consider its digestive function subordinate to its water-holding one. Ellenberger views the cæcum as a bowel for the digestion of cellulose, where by churning, maceration, and decomposition, this substance is dissolved and rendered fit for absorption, and he likens it to the stomach of ruminants and the crop of birds. He further considers that the cæcum exists owing to the small size of the stomach, and the rapidity with which the contents are sent along the small intestines. His experiments demonstrated that the entire 'feed' reached the cæcum between 12 and 24 hours after entering the stomach, that it remained 24 hours in the cæcum, and that during this time 10 to 30 per cent. of the cellulose disappeared.

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* We once found the cæcum acid.

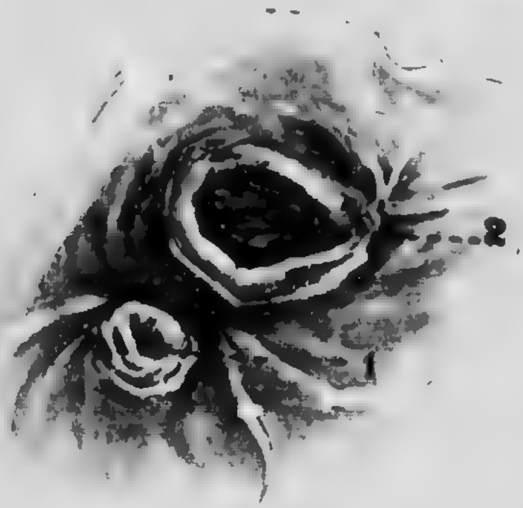

FIG. 50.—THE OPENING OF THE ILEUM AND COLON IN THE CÆCUM.

1, The ileum; 2, the colon. In the figure the openings are represented close together, but even when stretched apart they are less than 4 inches distant.

The digestion of cellulose is no doubt a very important matter, especially as we know that the poorer the food the more cellulose digested; but we are not prepared to admit that food necessarily remains in the cæcum 24 hours, and we believe that cellulose digestion occurs principally, though not entirely, in the colon, and further, that it is not absolutely necessary the material should remain in the cæcum, but that it may pass on at once to the colon. Our experiments on digestion have shown that ingesta may reach the cæcum 3 to 4 hours after entering the mouth, and we are quite clear on the point that oats may travel some considerable distance along the colon in 4 hours from the time of being consumed, though this is regarded as exceptionally rapid. A horse which had never had maize and had not tasted oats for two or three years, was fed first with 2½ lbs. of maize, and 17 hours later with 4 lbs. of oats. The animal was destroyed 4 hours from the time of commencing to eat the oats. Much maize and a few oats were found in the pelvic flexure of the colon, and a certain proportion of maize and a quantity of oats in the stomach. In 21 hours the small ration of 2½ lbs. of maize was distributed between the stomach and pelvic flexure of the colon, which is a very large area. In 4 hours the oats reached the same point in the bowel that the maize had arrived at; this is exceptionally rapid, but this experiment supports two points it is desired to emphasize, viz., the difficulty in getting the stomach to empty itself completely, and the rapid transit of material through the small intestines.

Colin believes that in the cæcum starch can be converted into sugar, fats emulsified, and the active absorption of assimilable matters occur.

The Colon.—The direction taken by the colon of the horse is remarkable. It commences high up under the spine on the right side, its origin being very narrow, but it immediately becomes of immense size; it descends towards the sternum, and curving to the left side, rests on the ensiform cartilage and inferior abdominal wall. The colon now ascends towards the pelvis, and here makes a curve, the bowel becoming very narrow in calibre: the pelvic flexure having been formed, the intestine retraces its steps towards its starting point. Running on top of the previously described portion it descends towards the diaphragm, gradually growing larger in calibre, and then ascends towards the loin, being here of immense volume—in fact, at its largest diameter; it then suddenly contracts, and forms the single colon (Figs. 51 and 52). The object of the difference in the volume of the double colon appears to be for the

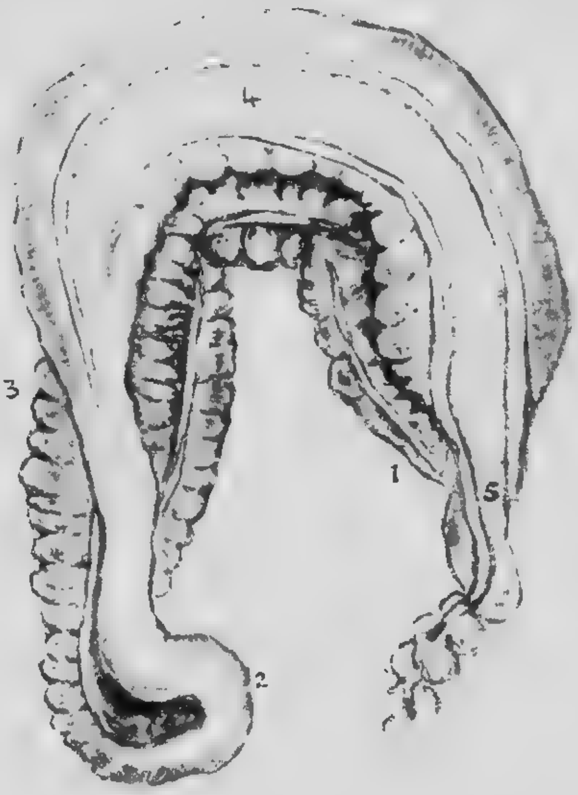

Fig. 51.—The Double Colon looked at from Above (modified from Müller).

1, The first colon, the cæcum being removed; 2, the pelvic flexure, the bowel being narrow; 3, the colon suddenly enlarges; 4, its diaphragmatic flexure; 5, the single colon. Several of the bands are seen; note also the sacculated and non-sacculated portions of the bowels.

convenience of its accommodation in the abdominal cavity.

The double colon may for the purpose of description be divided into four portions: the ingesta in the first and third descend, in the second and fourth ascend. It is found that the physical characters of the contents are not the same throughout. In the first colon the food is fairly firm, and the particles of corn, etc., can be readily recognised; in the second colon the material is becoming more fluid, whilst at the pelvic flexure the contents are invariably in a liquid pea-soup-like condition, and the particles of which they are composed are not readily recognised. In

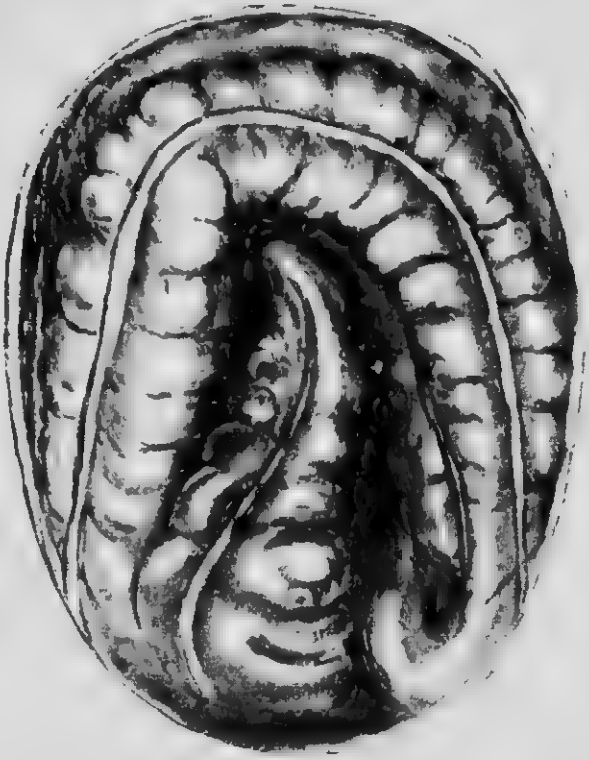

Fig. 52.—Position of the Cæcum and Double Colon on the Floor of the Abdomen seen from Below.

The point of the cæcum is directed towards the sternum.

the third colon the material becomes firmer, but only slightly so, and bubbles of gas are being constantly given off from its surface; in the fourth colon the entire ingesta are like thick soup, and the material composing them is in a finely comminuted condition, the surface being covered with gas bubbles. For the first foot or so of the single colon this condition is maintained, when quite suddenly the contents are found solid and formed into balls. The remarkable suddenness of this change is invariable in a state of health, and indicates either most active absorption, or that the contents are subjected to great compression. The entire contents of the colon are yellow in colour or yellowish green, rapidly becoming brown or olive-green on exposure to the air; the colour being due to the chlorophyll of the food. The contents of the colon are normally alkaline throughout; we once, however, found them acid.

Digestive Changes.—The changes food undergoes in the large intestine have never excited the same interest as those in the small. The absence of any secretion from the large bowel other than the succus may help to account for this, and may also assist in explaining why the large bowels have been regarded in the light of reservoirs for ingesta, rather than as active centres of digestion. As a matter of fact, the large intestines of the horse are actively employed in dealing with cellulose, not by means of any known enzyme peculiar to the body, but rather by the process of bacterial disintegration, the result of decomposition. It is known that bacteria may hydrolize cellulose and render it fit for absorption. In the case of oats we mentioned, p. 171, that they probably furnished their own cellulose enzyme, but this has not been proved for all vegetable material. The cellulose of hay is, probably, only extracted after prolonged maceration in the large intestines and the subsequent attack of bacteria. By some, it has been considered that the epithelial cells of the intestine are capable of dealing with cellulose, but on this point no definite statement can be made. Cellulose yields energy to the body on oxidation, but there is another reason for the extensive preparations made for its digestion in herbivora, viz , the cellulose encloses the proteid, starch, and fat of vegetable substances in a frame-work, and until this is broken down these substances cannot be acted upon. We know that considerable cellulose solution must occur before the material arrives at the large intestines, otherwise neither in the stomach nor small intestine could digestion occupy the prominent position it does. The digestion of proteid, fat and sugar are largely, though not entirely, dealt with in the stomach and small intestine, but there must be a certain amount of these substances so firmly locked up in their cellulose envelope that they are not liberated until after prolonged maceration and digestion in the large intestines, We may, therefore, safely assume that proteid, fat, starch, and cellulose are capable of being acted upon and absorbed from the large bowels of the horse.

As the result of cellulose digestion carbonic acid and marsh gas are formed in equal volumes. We have in our description of the large bowels drawn attention to the appearance of the cæcum and fourth portion of the double colon, with their pea-soup-like contents, on the surface of which gas bubbles are constantly breaking. It may well be that these two places are the active seats of the final transformation of cellulose, the cæcum dealing with that which has already been acted upon in the stomach and small intestines, and the fourth colon being concerned with the more refractory cellulose, which has required prolonged maceration in the large intestines before becoming capable of solution. This is rather supported by the remarkably rapid change in the character of the contents in the single colon, the pea-soup-like condition giving way, in the space of a few inches, to the appearance presented by ordinary normal fæces.

The large intestines cannot exist entirely for the solution of cellulose. There are other processes going on, chief of which is the bacterial attack on the unabsorbed proteid products of the small intestines. The small intestine may be regarded as free from putrefactive processes, in fact it is only towards the ileum that the unpleasant products of pancreatic digestion can be detected. In the large intestine, on the other hand, putrefactive processes are evident throughout; the bacteria are here engaged, among other things, in attacking the unabsorbed products of proteid digestion and reducing them to simpler end-products, such as peptones, proteoses, amido-acids, indol, skatol, phenol, phenyl-proprionic, phenyl-acetic and fatty acids, with the evolution of CO_2, H_2, H_2S, and CH_4. These end-products are got rid of either through the fæces, or they are absorbed into the blood, taken to the kidneys, and combined with sulphuric acid are got rid of through the urine; especially is this the case with phenol, indol, and skatol.

As the material moves towards the rectum it becomes drier and drier, and more thoroughly formed into balls by the action of the bowel-sacs, which squeeze the mass into a round or oval shape. The contents of this portion are still alkaline, or slightly so. As we approach the anus a distinctly acid reaction is obtained on the surface of the fæces, though at this time the interior of the ball may be, and often is, alkaline; the converse of this may also be obtained. In the rectum the single balls collect in masses, to be forced out of the body at the next evacuation. The reaction of this mass is acid, and the colour depends on the food, being, on an ordinary diet, of rather a reddish-yellow or brownish tint due to altered chlorophyll.

Absorption from the single colon and rectum is rapid; the marked change in the physical character of the fæces is evidence of this. Animals may also be killed by the rectal injection of strychnine; narcosis can be produced by the rectal administration of ether, and life may be supported, at any rate for a short time, by means of nutrient enemata.

Intestinal Digestion in Ruminants.—Though intestinal digestion is so important in the horse, it would appear in ruminants to occupy a subordinate position. It is curious why in one animal the changes should occur at the anterior, and in the other at the posterior part of the digestive tract, but this difference in the arrangement for digesting cellulose depends upon one being capable of rumination and the other not. The rumen of the ox corresponds to the large intestines of the horse. The intestines of the ox are of extreme length but small in calibre; they are half as long again as those of the horse, and it would appear that their chief function is that of absorption. Their arrangement, especially that of the large intestine, is most singular. The small intestines are hung in convolutions on a mesentery; they are narrow in diameter and about 120 feet in length. The large intestines are about 30 feet in length, also narrow and without muscular bands or puckerings as in the horse; the colon is arranged in a remarkable spiral manner between the folds of the mesentery (see Fig. 53). It is in this immense length of absorbent surface that the food substances capable of being utilized are taken up. It is clear, however, that certain digestive changes occur in the small intestines, into which, as in other animals, the pancreatic and biliary fluids are poured. Here the proteids which have escaped the stomach, and the fats and starches

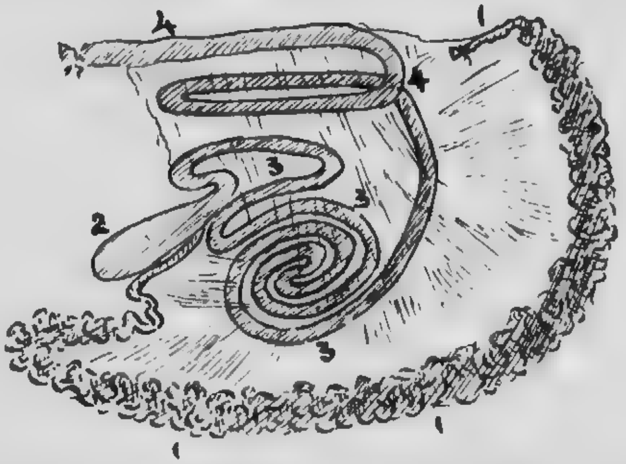

FIG. 53.—SCHEMATIC ARRANGEMENT OF THE INTESTINES OF THE OX.

1, The small bowels; 2, the cæcum; 3, the 'spiral' colon; 4, the single colon.

are rapidly changed and rendered fit for assimilation; the altered cellulose in all probability only finds its way here when fit for absorption after its digestion in the rumen.

Intestinal Digestion in other Animals.—**In the pig** intestinal digestion is said to be of short duration, and absorption very rapid. **In the dog** the material passes out of the stomach slowly and only in small quantities into the small intestines, which are usually found collapsed. It is in the small intestines of this animal that the chief digestion occurs, as the large bowels are rudimentary.

In the sheep, ox, pig, and dog, the reaction of the contents of the small intestines is acid anteriorly and alkaline towards the ileum; probably in all animals the contents of the large intestines are alkaline in reaction.

Munk gives the following statistics respecting the intestinal canal. In the tiger and lion the whole digestive tract is 3 times the length of the body, in the dog 5 times, man 9 times, horse 12 times, pig 16 times, and ox 20 times. The comparative shortness of the intestinal canal of the horse is compensated by its enormous capacity, which is 352 pints; in the ox 140 pints, pig 47 pints, dog 14 pints. The area of the intestinal tract is also given by the same observer—horse 550 square feet, ox 160 square feet, pig 32 square feet, and dog 5½ square feet (M'Kendrick).

Movements of the Intestines.—The movements of the intestines are brought about by the involuntary muscle composing its wall. This muscle in the small intestines is arranged in two sheets in a circular and longitudinal manner, while in the large intestines narrow bands of pale muscle of considerable length take the place of the ordinary longitudinal layer, and may be found on all parts where the tube is sacculated. In fact, one function of the bands is to bring about the sacculated condition of the canal, an important arrangement whereby economy of space is effected with no loss of surface.

The sacculated condition of the double colon is confined principally to the first and second and fourth portions. The third portion especially at the pelvic flexure is free from sacculations, and the fourth portion is not so liberally puckered as the first and second. On the first colon there are four bands, on the second colon there are also four, three of which disappear at the pelvic flexure; on the third portion there is only one band, while on the fourth colon there are three (see Fig. 54, also Figs. 51 and 52). In the large intestines the longitudinal layer of fibres is confined to the muscular bands, so that the great bulk of the wall consists of circular muscle only. The longitudinal bands shorten the bowel, but the main work in pressing the contents along is performed by the circular layer. The bands, in fact, are numerous where the intestine is large, and reduced in number where the bowel becomes smaller. This arrangement suggests that they may under suitable conditions produce an irregularity of pull, and we can see no other explanation of displacement of the large intestines of the horse (a matter dealt with more fully at the end of this chapter) than through the medium of these muscular bands.

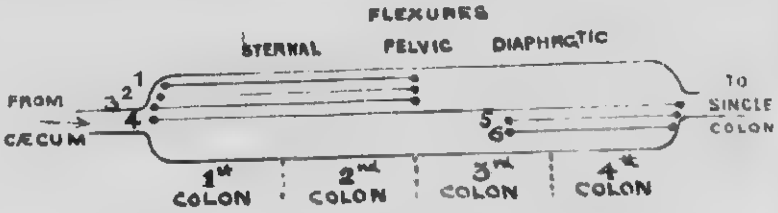

FIG. 54.—SCHEMATIC ARRANGEMENT OF THE MUSCULAR BANDS ON THE DOUBLE COLON.

The colon is supposed to be opened out into a straight tube. Bands 1, 2, and 3 run from the first colon to the pelvic flexure; one of the three actually comes from the apex of the cæcum. No. 4 is the only band running the whole length of the bowel. Nos. 5 and 6 originate in the region of the third colon, and finally run on to the single colon.

The muscular movements of the large intestine are slower than those of the small bowels; possibly one reason for this may be that the food has to remain a longer time in contact with the absorbing surface, viz., for at least forty-eight hours, and for as long as four days. The peristaltic movement of the small intestines is quite distinct from that of the large; the one ends at the ileum, the other begins at the cæcum.

The muscle of the intestinal wall causes the movement known as *peristalsis*, which normally passes in the direction stomach to rectum. Relatively quick in the small intestines it becomes slower and more deliberate in the large, but the wave has always the one object in view, viz., to press the ingesta onward. A wave of contraction passing the reverse way, viz., in the direction of rectum to stomach, is known as *antiperistaltic*: such a movement is considered abnormal, but in the horse, according to the observations of Colin, antiperistalsis of the small intestines is a natural condition. Some physiologists recognize antiperistaltic movements of the large intestines as being normal in certain animals, producing a to-and-fro movement of the contents, but it is generally thought that in the small bowels antiperistalsis is only present under abnormal circumstances. If antiperistalsis be admitted for the large bowels, we see no difficulty in extending it to the small, especially in view of Colin's positive statement that it occurs. The peristaltic wave depends upon a something peculiar to the bowel wall, for if a piece of small intestine has been experimentally reversed, so that the portion originally nearest the stomach is made to occupy a position farthest away from it, it is found that the peristaltic wave in the reversed segment is still in the original direction instead of in the new direction. The actual mechanism involved in a peristaltic contraction, according to Starling and Bayliss, is as follows: The circular muscle on the stomach side of the bolus contracts, while that on the far side is relaxed for some distance, so that the advancing wave drives the bolus into a relaxed portion of bowel. If a solution of cocaine or nicotine be applied to the intestinal wall these movements cease, from which it is argued that they are probably due to local ganglia.

Another movement quite different to the above is the *pendular*, which shows itself by a gentle swaying to and fro of the different loops of bowel, caused by a simultaneous contraction of both muscular coats. This movement is not stopped by cocaine or nicotine, from which it is reasoned that the nervous ganglia have nothing to do with it. These pendular movements, which are rhythmical and as regular as the heart-beat, are regarded by Starling and Bayliss, who first described them, as being of the greatest importance, as they cause the material under digestion to be mixed thoroughly with the secretion, and bring it in contact with the wall for absorption. While these rhythmic contractions are in operation the food is not pressed onwards, but remains in the same region of the bowel, undergoing, however, repeated divisions. We have not succeeded in observing the pendular movements in the horse.

In the first and third portions of the colon the ingesta travel by their own gravity; in the second and fourth portions they travel against gravity, as in the cæcum. As the first and fourth and second and third portions of the colon are united, the curious results follow that material is passing along each section apparently in two opposite directions. The frequency of intestinal affections in the horse causes the canal to be of exceptional practical interest. When the cæcum is found completely inverted into the colon, as if a hand had passed through the colo-cæcal opening, laid hold of the apex of the cæcum and drawn the entire bowel within the first portion of the colon, it is then that the question of muscular movements so strongly presents itself. Or take what is far commoner and equally fatal, viz., displacement or actual twist of the large bowel, or a complete twist of the small intestine, leaving the bowels in such indescribable confusion that the parts cannot be unravelled, even when removed from the body! It is impossible to believe that muscular action of the intestines is free from all blame in the production of these lesions. It is easier to understand a twist of the small intestine apart from muscular action than it is to understand displacement or actual twist of the large intestine. A loop or coil of small intestine may be so distended by gas or ingesta as to become twisted, but it is more difficult to imagine either of these conditions producing twist or displacement of the large intestines, and it becomes a question, as we have previously said, how far the action of the muscular bands of the bowel may have a contributing influence. That great force is necessary is undoubted, bearing in mind the difficulty, if not impossibility, of restoring the parts to their position post-mortem, or endeavouring after death to reproduce the lesions experimentally. These matters will be referred to again.

Nervous Mechanism of the Intestinal Canal.—Two distinct impulses are conveyed by the intestinal nerves, viz., those for contraction and for inhibition. In the anterior part of the tract the former function is mainly or entirely carried out by the vagus, stimulation of which is found to cause active contraction of the small intestines. Contraction of the large intestines is effected through branches of nerves which issue from the sacral portion of the cord, and pass with the nervi erigentes to the hypogastric plexus. From this plexus fibres run in the coats of the large intestines, producing on stimulation much the same results as the vagus, viz., active contraction of both circular and longitudinal coats.

Stimulation of certain branches of the sympathetic nerve stops or inhibits the contractions produced by stimulation of the vagus, hence the term 'inhibitory.' The inhibitory nerves of the small intestine are derived from the dorso-lumbar portion of the cord, pass by the rami communicantes (*rc.*, Fig. 55) to the main sympathetic chain, *Sy.*, and from thence through the large and small splanchnic nerves to the solar plexus, from which the final distribution to the intestines is made. The inhibitory fibres for the large intestines are derived mainly from the lumbar cord through *rc.* and *Sy.* (Fig. 55) to the inferior mesenteric ganglion. From this ganglion inhibitory fibres are given off to both longitudinal and circular coats.

Contractions of the bowels and peristalsis can occur after all nerves leading to the intestines have been divided; this points to the existence of local ganglia, and such may be

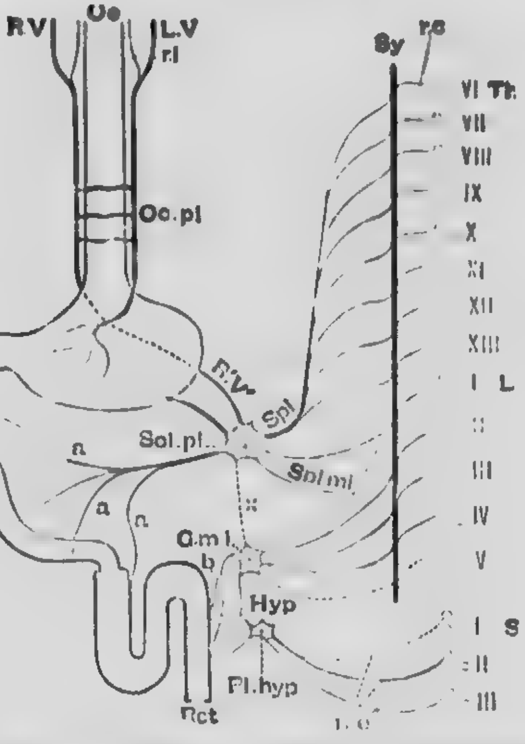

Fig. 55.—Diagram to illustrate the Nerves of the Alimentary Canal of the Dog (Foster).

(The figure is very diagrammatic and does not represent the anatomical relations.)

Oe. to *Rct.* The alimentary canal from the œsophagus to the rectum.
LV. Left vagus nerve ending on the front of the stomach. *rl.* Recurrent laryngeal supplying upper part of œsophagus. *R.V.* Right vagus joining left vagus in the œsophageal plexus *Oe. pl.*, supplying the posterior part of the stomach, continued as *R'.V'.* to join the solar plexus, *Sol. pl.*, *here represented by a single ganglion*, and connected through *x* with the inferior mesenteric ganglion (or plexus). *G. m. i. a*, *a*, *a*, branches from the solar plexus to stomach and small intestines, and *b* from the mesenteric ganglion to the large intestines.
Spl. Large splanchnic nerve arising from the thoracic ganglia of the sympathetic *Sy.* and rami communicantes *r.c.* of the dorsal nerves.
Spl.mi. Small splanchnic nerve. Both the large and small splanchnics join the solar plexus and thence make their way to the alimentary canal, supplying the small intestine with inhibitory impulses.
G.m.i. Inferior mesenteric ganglion formed by nerves running from the dorsal and lumbar cord. From this ganglion inhibitory nerves are given off to the large intestines.
n.e. Nervi erigentes arising from the sacral cord and proceeding to the hypogastric plexus. *Pl. hyp.* From this plexus impulses of a motor kind are supplied to the large intestines.

found in the intestinal wall. The intestinal movements are automatic and self-regulated, though they can be provoked by both chemical and mechanical stimuli. The normal stimulus to peristalsis is the passage of ingesta along the canal. In the dog even the sight of food is said to promote peristalsis. Gases such as CO_2, H_2S, and CH_4, and organic acids such as acetic, proprionic, caprylic, etc., act as stimuli and promote contraction, which is a fortunate circumstance, as they are normal to the bowel in consequence of bacterial activity. Oxygen gas, on the other hand, inhibits movements, and, as a matter of fact, we know that oxygen gas normally does not exist, or only in traces, in the gaseous contents of the bowels. Cutting off the blood-supply to the bowels causes violent contractions, which occur again when the circulation is re-established; the former is of interest in those cases of twist where the blood-supply is wholly or partly interfered with.

Under normal conditions the mind is not conscious of peristaltic movements, but when these become very energetic pain is produced. Under the influence of nervous excitement rapid and frequent evacuations of the bowels may take place in both cattle and horses. So rapid may the evacuations be that in the horse, in a short time, the whole of the rectum and single colon are unloaded. Ordinary exercise is always an important cause of peristalsis, and hence an actual means of unloading the rectum.

As previously remarked, the normal stimulus to peristalsis is the presence of ingesta in the canal. In the feeding of herbivora bulk is essential, they cannot live in a state of health on concentrated food alone. Their intestines need bulk, if only in order to maintain peristalsis. Bunge has shown that if cellulose be withheld from the diet of rabbits they die from intestinal obstruction. It is the cellulose and lignin in the diet of herbivora which largely provide the needful stimulus to peristalsis.

Gases of the Intestines.—The largest amount of gas found in the intestinal canal is in the cæcum and colon; the small intestines naturally contain very little, frequently none, whatever is formed there being probably rapidly passed into the large bowels. In the large intestines marsh-gas commonly exists, forming with carbonic acid the bulk of the gases present. The pathological conditions arising in the large bowels of horses, and in the rumen of cattle, as the result of fermentation—particularly of green food—and the enormous size to which these animals may in consequence be distended, are matters of common clinical experience. In both horse and ox the gas may generally be ignited a short distance away from the cannula which has been passed to give relief, the marsh-gas igniting readily on meeting with the proper proportion of oxygen. The whole of the chemical changes in the intestinal canal are carried on in the absence of oxygen; the gases which are produced depend mainly on the nature of the food, green material producing marsh-gas and carbonic acid, leguminous matters producing sulphuretted hydrogen and hydrogen.

The Fæces.—The fæces consist of that portion of the food which is indigestible, together with that part which though digestible has escaped absorption; mixed with these are water, colouring substances, mucin, organic matters in great variety, inorganic salts, bile pigment, volatile fatty acids, remains of digestive fluids, organisms, etc.

The composition of the fæces depends largely on the diet. The following table from Gamgee* can only give a general idea of their nature:

APPROXIMATE COMPOSITION OF THE FÆCES OF THE

	Horse.	*Cow.*	*Sheep.*	*Pig.*
Water - -	76·0	84·0	58·0	80·0
Organic matter -	21·0	13·6	36·0	17·0
Mineral " -	3·0	2·4	6·0	3·0
	100·0	100·0	100·0	100·0

Considerable differences exist amongst animals in the consistency of the fæces; they are moderately firm in the horse, pultaceous in the ox, and hard in the sheep. These differences depend upon the amount of fluid they contain. In the pig they are human-like and very offensive; in the dog they are soft or hard, dark or light, depending on the diet, the mineral matter of bones producing the light-coloured excreta. It is necessary to remember that the proportion of fluid in the fæces does not depend upon the amount of water which is drunk, but rather on the character of the food, the activity of intestinal peristalsis, and the energy with which absorption is carried on in the digestive canal. Succulent green food in horses produces a liquid or pultaceous motion; other foods, such as hay and chaff, have a constipating effect, the fæces being large and firm; excess of nitrogenous matter in the food produces extreme fœtor of the dejecta, and frequently diarrhœa, probably due to putrefactive processes. Nervous excitement frequently induces a free action of the bowels, accompanied by liquid fæces.

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* 'Our Domestic Animals in Health and Disease,' p. 253.

Fæces always float in water so long as cohesion is maintained. The colour of the fæces in the horse is yellowish or brownish-red, in the ox greenish-brown; they rapidly become darker on exposure to the air. When the animal is grass-fed the fæces are green, and when a horse is fed wholly on corn they become very yellow and like wet bran in appearance. The colour of the fæces of animals receiving hay or grass is due to altered chlorophyll. The fæces of the horse are moulded into balls in the single colon. They are always acid in reaction, the acidity probably depending upon the development of some acid from the carbo-hydrates of the food.

Fæces contain lignin amongst the indigestible portion of the ingesta, a proportion of cellulose, husks of grains, the downy hair found on the kernel of oats, vegetable tubes and spirals, starch and fat granules, gums, resins, chlorophyll, etc.; unabsorbed proteid, carbo-hydrate and fatty matters; products of digestive fermentation, such as lactic, malic, butyric, succinic, acetic, and formic acids; leucin, tyrosin, indol, skatol, and phenol; biliary matters and altered bile pigment—stercobilin—which gives the colour to the dejecta in the dog but not in herbivora; and, lastly, mineral matter in varying proportions. In the dog portions of muscle fibre, fat cells, tendinous and fibrous tissue, are found in animals fed on flesh.

Of the *inorganic matter* silica exists in largest amounts in herbivora, then potassium and phosphates; sodium, calcium, magnesium, and sulphates, form a smaller but still important proportion. The horse excretes but little phosphoric acid by the kidneys, but considerable quantities pass with the fæces in the form of ammonio-magnesium phosphate. This salt is derived principally from the oats and bran of the food, and it frequently forms *calculi* through collecting in the colon and becoming mixed with organic substances. Other intestinal calculi are formed from lime deposits in the bowel, while collections of the fine hairs from the kernels of oats become encrusted with ammonio-magnesium phosphate and form oat-hair calculi. In the Persian wild goat and certain antelopes intestinal concretions are found known as Bezoar stones, formerly much used in medicine and as antidotes to poison. There are two varieties of calculi, one olive green, the other blackish green. The first melts when heated, emits aromatic fumes, and consists chiefly of an acid allied to cholalic acid. The chief constituent of the second variety is an acid derivative of tannic acid, which indicates their origin from food substances. Stomach calculi have not been unknown in the horse, while in cattle, as the result of licking each other, 'hair balls' are common objects.

The following table by Roger gives the mineral composition of the fæces in every 100 parts of the ash:*

	Horse.	*Ox.*	*Sheep.*
Sodium chloride	·03	·23	·14
Potassium	11·30	2·91	8·32
Sodium	1·98	·98	3·28
Lime	4·63	5·74	18·15
Magnesium	3·84	11·47	5·45

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* Quoted by Ellenberger.

	Horse.	*Ox.*	*Sheep.*
Oxide of iron	1·44	5·22	2·10
Phosphoric acid	10·22	8·47	9·10
Sulphuric acid	1·83	1·77	2·69
Silica	62·40	62·54	50·11
Oxide of magnesium	2·13	—	—

Roger observes that the ash of the fæces of herbivora contains scarcely any alkaline carbonates.

The **amount of fæces produced** in 24 hours varies with the quantity and nature of the food given. We have observed that on a diet consisting of 12 lbs. of hay, 6 lbs. of oats, and 3 lbs. of bran, the average amount of fæces passed by fifteen horses during an experiment lasting seven days amounted to 29 lbs. 13 ozs. in 24 hours, the fæces being weighed in their natural condition, viz., containing 76 per cent. water; the dry material of this bulk of fæces is about 7¼ lbs. More fæces are passed during the night than during the day; in the above experiment, during the 12 hours (6 p.m. to 6 a.m.), the average amount of fæces per horse was 18 lbs. 3 ozs., whilst from 6 a.m. to 6 p.m. the amount was 11 lbs. 10 ozs. The largest amount of fæces we have known a horse produce was an average of 73·3 lbs. (weighed in their natural state) in 24 hours; the diet consisted of 12 lbs. of oats, 3 lbs. of bran, and 28 lbs. of hay. In an experiment carried on for several months with different horses all receiving 12 lbs. hay and varying proportions of bran and oats, the average daily amount of fæces was 24 lbs. A horse will evacuate the contents of the bowels about ten or twelve times in the 24 hours, and the food he consumes takes on an average four days to pass through the body.

In the ox the amount of fæces is between 70 lbs. and 80 lbs. in the 24 hours. In the sheep it varies from 2 lbs. to 6 lbs. daily; in swine 3 lbs. to 6 lbs., depending on the nature of the diet.

The **odour of fæces** is distinctly unpleasant, due to the presence of indol and skatol; in disease they are often extremely fœtid, and occasionally horrible.

The act of **defæcation** is performed by a contraction of the rectum assisted by the abdominal muscles, the glottis being closed. In the horse the contraction of the rectum alone is sufficient to expel its contents; this is proved by the fact that this animal can defæcate while trotting, showing there is no necessity to fix the diaphragm and hold the breath, though at rest this does occur. In consequence the rectum of the horse can exercise extraordinary power; the hand and arm may be rendered almost numb by the pressure it can exert. The mass driven backwards under this force causes the sphincters to dilate, sometimes to an astonishing degree, and as the last trace of material is exuded, the contraction of the rectum is so great that it forces some of the mucous membrane externally, which may be temporarily imprisoned by the contracting sphincters. The muscle of the rectum receives both motor and inhibitory fibres, as previously described. Its extraordinary power in the rectum in the horse may partly be due to the horizontal position of the body; no crouching of the body occurs during the act of defæcation, such as occurs, more or less, with all other domesticated animals. The rectum has the whole work to perform single-handed, even as we have shown above, without the assistance of the diaphragm or abdominal muscles.

Two sphincters close the rectum in all animals, an external of voluntary and an internal of involuntary muscle; they are presided over by a centre in the cord. If this is destroyed the rectum remains uncontracted, and the sphincter flabby; in the dog the cord may be destroyed in the lumbar region without interfering with the act of defæcation, which is then carried on by a reflex mechanism.

Meconium is the dark-green material found in the intestines of the fœtus. It consists of biliary acids and pigments, fatty acids and cholesterin, while salts of magnesium and calcium, phosphates and sulphates, sodium chloride, soda, and potash are also found in it. Meconium is the product of liver excretion.

Pathological.

The diseases of early life in the horse are mainly situated in the chest, while those of the adult period are practically confined to the abdominal viscera, principally the intestines. The term colic appears to be indissolubly associated with the horse, and it becomes a question of the greatest practical and physiological interest to ascertain the reason why digestive disturbances are so common and so frequently mortal. There are certain obvious explanations of the fact, but neither singly nor combined are the accepted ideas capable of explaining some of the mysteries surrounding the origin of these diseases.

When muscular spasms of the intestines occur the disease is spoken of as **colic**; in many cases the pain which is exhibited is in no respect due to muscular spasm, and is only a symptom. Still, by far the majority of intestinal cases are of this kind, viz., simple muscular spasms of some part of the digestive tract, but of which part we are certainly ignorant. It is obvious that either the stomach, the small or the large bowels may be so affected, but there are no definite symptoms which enable a positive diagnosis of location to be established. It is important to bear in mind the possibility of spasm of the muscular walls of the stomach, for there can be no doubt it is generally overlooked, and the intestines almost universally blamed. The evidence supporting the view we take of the liability of the stomach to disorder is afforded by the frequency of rupture of the organ, not that the rupture is due to spasm of the walls, but that the spasm is caused by stomach trouble, the rupture following as a sequel, as detailed on p. 153. It is, however, admitted that stomach spasm is far less common than spasm of the intestinal portion of the tract. We would here emphasize the facts set forth on p. 178, of the general inability of the horse to vomit, and the serious bar this proves to relief, so much so that it is hardly going too far to say that if the animal could vomit ruptured stomach would practically be unknown, and stomach trouble generally a matter of comparatively slight importance.

In connection with intestinal trouble, we are unable to say what proportion the cases affecting the small intestines bears to those affecting the large. We cannot during life distinguish colic of the one from colic of the other. Still, there are good grounds for thinking that the large bowels are more frequently affected than the small, and for the following reasons:

1. Ingesta pass rapidly through the small intestines—so rapidly indeed that, as mentioned at p. 190, these bowels are nearly always found empty at ordinary post-mortem examinations, or the contents in such a fluid condition that it is not reasonable to suppose that they remain there long, from what we know of the behaviour of fluids generally in the anterior part of the digestive tract.

2. On the other hand, the large intestines always contain ingesta, for the material passes along it very slowly, so that of the three or four days occupied in accomplishing the journey from mouth to anus all but a few hours is spent in the large intestines. It is reasonable, therefore, to assume that in cases of pure uncomplicated disordered muscular action of the bowels, the large intestine in the majority of cases is at fault.

Colic is not fatal, though Percival described such a case. Our experience leads us to believe that death from pure spasm of the bowels is unknown, and we would emphasize the point not only for the sake of accuracy, but as of value in prognosis. We believe that in any case returned as dying from colic, a more extensive search would have revealed some fatal lesion. There is no reason for believing that the pain of colic *per se* is capable of causing death.

If this be accepted, and it is fortunately capable of proof, it considerably narrows the causes of death from intestinal affections, and groups them mainly under two heads: (*a*) Inflammation of the bowels, and (*b*) displacement of the bowels.

Enteritis, by which name inflammation of the bowels is known, is spoken of as a common disease of the horse, but here again we join issue with accepted doctrines and urge that it is an uncommon disease. Further, that in the large majority of so-called cases of enteritis, some displacement of the bowels with interference to the circulation has occurred. That uncomplicated enteritis may exist is not disputed, but we urge its relative infrequency, and press the point that what looks like inflammation is more often strangulation. When a deep purple thickened coil of intestine is found on opening the abdomen, such a case is not enteritis. The colour indicates that the blood-supply has been imprisoned as the result of strangulation, and an identical appearance would have been obtained by ligaturing the bowel. When half the double colon is found purple, thickened, filled with blood-stained fluid ingesta, the wall of the bowel being friable and its mucous membrane purple, then however much we may be tempted to speak of it as enteritis, it certainly is not this disease, but strangulation. Enteritis must be reserved for that condition of bowel in which the mucous membrane alone is inflamed. Such a bowel may give no external indication of trouble; the general vascular supply is not interfered with; the full intensity of the trouble falls on the mucous membrane, and such a condition may be experimentally produced by the administration of an irritant poison. It is probable that in the horse the majority, if not all the cases, of pure enteritis met with, are due to a poison produced during the process of digestive metabolism (see p. 231). That the presence of an irritant without a poison has no such effect, is abundantly proved by the pounds of sand and gravel horses may carry in their intestines for months, perhaps years, without producing any apparent ill effect, certainly without producing enteritis. Similarly, gastritis excepting as the result of poison is practically unknown.

Our object in the above remarks is to focus attention on he defects in clinical observation, and to attempt a physiological analysis of the most frequent, the most fatal, and by far the most acutely painful and distressing group of diseases that any animal is exposed to. There is nothing in the whole range of comparative pathology, including the diseases of man, which compares in violence, suddenness, and mortality with digestive diseases of the horse. We have attempted to show how physiology is capable of enabling us to steer along a moderately exact course, for it is certain that unless we are agreed regarding the nature of the lesions found at *post-mortem* examination, we cannot reach that goal which is the object of our existence as a profession, and of which physiology is only the humble handmaid.

What is the most common cause of death among horses from intestinal affections, whether affecting the large or small bowels? There is only one answer to this, and time and careful enquiry will prove its accuracy. The answer is **Strangulation** of the bowels, partial or complete. This strangulation is capable of physiological analysis. The most unobservant person cannot overlook a bunch of small intestines so tied together as to defy all attempts at unravelling, even when out of the body, but it takes a little careful observation to detect displacements of the large intestine.* The size, weight, and peculiar disposition of the double colon should have secured it immunity from any form of displacement; looked at in the abdomen, it appears impossible for any force short of some mysterious power to be able to influence the position of the bowels, yet we know they are capable of being twisted as easily as if they were made of cotton. We know also that one portion may be thrust into another, in just the same way as a telescope collapses, and that a voluminous bowel like the cæcum may become completely inverted, and found within the colon, though to get there it has to pass through an opening only an inch or two wide. So remarkable indeed are these lesions that they cannot always be imitated after death, and, as mentioned above, it is impossible to untie many complicated knots in the small bowels, even when the organs have been removed from the abdomen.

The actual mechanism which brings about twists of the large and small intestines is disordered muscular action; the factor responsible for telescoping intestines is disordered muscular action, and disordered muscular action is the result of disordered nervous action. For telescoping to occur, one portion of bowel must first contract until it becomes but a mere shadow of its former self; the contracted part must then be drawn within the dilated. A different cause is at work to produce a twist of the small intestine; this as we previously indicated is tympany of the bowel, while in the case of the large intestines the muscular action must be capable of causing the bowel to perform a revolution more or less complete, and in this way reversing its position. We cannot attempt to indicate the exact disordered action which occurs; this question would require to be worked out on the living subject. The colon and cæcum are most liberally supplied with bands (Figs. 48, 49, 51, 52, and 54), and it does not appear to us to be beyond the bounds of reasonable probability that these play a most important part in the production of displacements of the large intestines. The cause of the disordered nervous action which leads to this may, from its physiological interest, be briefly dealt with. Apart from such obvious explanations as errors in feeding (see in this connection pp. 170, 237), the most common cause of derangement of the muscular action of the digestive canal is *work*. It is this which accounts for the majority of colic cases occurring towards the end of the day, the frequency with which the seizure occurs at or shortly after work, especially that of an exhausting nature, and the practical absence of colic among non-working horses. We have even known a horse in a cavalry charge rupture the ileum as completely as if the parts had been torn asunder by hand; and this, it will be remembered, is the thickest and stoutest portion of the small intestine, and the least likely to suffer laceration. The connection between such a lesion and an exhausting gallop is at present not very apparent, but the fact is undoubted.

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* From the point of view of equine pathology, one of the most valuable contributions made to veterinary literature by the late Professor Walley was his account of displacements of the colon in the horse (*Veterinary Journal*, vol. ix.). It was the first time in this country that the possibility of these immense bowels being twisted and displaced was ever described.

The whole subject is of profound practical interest, and more has been said on the matter than commonly falls to physiology to deal with, but the basis of exact clinical knowledge is sound anatomy and physiology, and we consider the physiological aspect of digestive disorders has not yet received adequate attention. We must bear in mind that the whole length of the digestive tract is a chemical laboratory concerned in the analysis of food-stuffs, isolating and retaining those which are of use, getting rid of those which are useless, and rendering harmless those substances capable of acting injuriously. Not only is it a laboratory where the above analytical operations are carried out, but it is also a factory where the chemical reagents necessary for this process are prepared beforehand. So thoroughly is the analysis performed, that the most complex bodies are broken down into the simplest products. Can it be wondered at, that the chemical processes may sometimes fail, and disorder result?

We see a faithful reflex of the laboratory processes in the disorders of the canal, the **diarrhœa** which is full of beneficence, the **impaction** which indicates a loss of muscular power and physical alteration of the contents, the acute **tympany** which announces active fermentation, the **rupture** which indicates the strain on the walls of the apparatus; these and others too numerous to be dealt with, and which no mere mention explains, give some idea of the penalty paid by horses for the doubtful privilege of domestication. The term 'digestion of a horse' has been framed in absolute ignorance of the real facts. There is no animal in which these organs are more readily disturbed, and none in which they are the subject of such acutely painful and mortal lesions.

The ruminant from the peculiarity of its physiological arrangement is far more liable to stomach than intestinal trouble; **tympany**, **impaction**, **paralysis**, and **inflammation** of one or more of the compartments are common. In spite of the size of the œsophagus impaction is frequent, in marked contrast to the horse, in which it is uncommon, while **calculi**, a special feature in the intestine of the horse, are found in the stomach of the ox, though brought about by very different causes. **Strangulation** of the bowels in the ox is not unknown, but limited to a special variety due to anatomical conditions. **Parasitic** trouble in all animals is a prominent pathological feature, the digestive canal from the mouth to the anus being liable to infection with numerous varieties of parasites, and it also forms the main channel of parasitic entry for other parts of the body.

CHAPTER VI

THE LIVER AND PANCREAS

SECTION 1.

The Liver.

IN considering the function of the liver it is necessary to bear in mind its peculiar blood-supply. Most glands of the body which are called upon to produce a secretion are furnished only with arterial blood for the purpose, but the liver is an exception to this rule; the entire venous blood returning from the splanchnic area, viz., the bowels, stomach, spleen, pancreas, etc., constitutes the material with which the liver is flooded. Such a mixture of blood derived from a peculiar and considerable area must be charged with many products, some the result of secretory activity, others the soluble constituents of the elements of food; or again, substances absorbed from the intestinal canal, which are bye-products produced during the gradual breaking-down of the food substances. It is from this blood that the liver performs its various functions, and one of the most evident, viz., the secretion of bile, will be dealt with first.

Bile.

The bile is a fluid of an alkaline reaction, bitter taste, a specific gravity in the ox of 1022 to 1025, in the sheep from 1025 to 1031, and in the horse 1005. The colour is yellowish-green or dark-green in herbivora, reddish-brown in the pig, and golden-red in carnivora. These differences in colour depend upon the character of the pigment present. Bile taken direct from the liver is relatively watery in consistence, that taken from the gall-bladder is viscid, due to admixture with nucleo-albumin during its stay in the latter receptacle. The secretion contains no proteid which is somewhat remarkable; biliary pigments, bile acids, fats, soaps, lecithin, cholesterin, and inorganic salts are found in varying quantities. By standing in the gall-bladder the solids are considerably increased, owing to an absorption of part of the water of the bile. The secretion in the horse contains no mucin, and, according to Ellenberger, there is very little mucin in the bile of sheep; what was believed to be mucin in ox bile, which conferred on the latter its ropy character, is now known to be nucleo-albumin.

The dried alcoholic extract of bile contains in the ox 3·58 per cent. of sulphur, sheep 5·71 per cent., and pig ·33 per cent. The gases found in bile are CO_2, and traces of O and N. The chief inorganic salts are sodium chloride and phosphate, besides which are found salts of calcium, magnesium, potassium, iron, with phosphoric and sulphuric acids; the sodium salts always exist in the largest proportion. The iron, which is found as phosphate, is probably derived from the hæmoglobin of the blood during the formation of the bile pigments.

The following table, showing the percentage composition of various biles, is mainly compiled from Ellenberger:

	Horse Bile.	*Ox Bile.*	*Dog Bile.*	*Pig Bile.*
Water	95	92·91	95·3	88·8
Solids	5	9·6	4·7	11·2
Bile acids Bile pigments Fat Mucin	—	8·8	4·1	10·1
Salts	—	1·8	·6	1·1

Percentage Composition of the Ash of Ox Bile.

Sodium chloride	27·7	Manganese peroxide	·12
Potassium	4·8	Phosphoric acid	10·45
Sodium	36·7	Sulphuric „	6·39
Calcium carbonate	1·4	Carbonic „	11·26
Magnesium	·58	Silica	·36
Iron oxide	·23		

The differences found in the composition of bile probably depend upon whether it be taken from the gall bladder or from a fistula, the former being the more concentrated.

The **Cholesterine** found in bile must be regarded in the light of an excretion; the liver is merely a convenient channel for getting rid of this waste product, which is collected from the many tissues of which it forms a part, brought to the liver, and eliminated through the bile by the bowels. It is found in very regular quantities, and forms the principal constituent of certain gall-stones; it is kept in solution in the bile by means of the bile salts.

Lecithin is another waste product of the body excreted from the system through the medium of the bile.

The **Bile Pigments** are two in number, **bilirubin** and **biliverdin**; the latter is produced by oxidation from the former. Bilirubin is the colouring matter of human bile and that of carnivora, whilst biliverdin is the pigment of the bile of herbivora. It is not uncommon to find both pigments in the same specimen of bile. These pigments are insoluble in water but soluble in alkalies; in the bile they are held in solution by the bile acids and alkalies. Bilirubin may be obtained from the gall-stones of the ox in the form of an orange-coloured powder, which can be made to crystallize in rhombic tablets and prisms. If an alkaline solution of bilirubin be exposed to the air it becomes biliverdin by oxidation, and this latter pigment by appropriate treatment may be obtained as a green powder. Both colouring matters of the bile behave like acids, forming soluble compounds with metals of the potassium group, insoluble ones with those of the calcium group (Bunge).

On the addition of nitric acid (containing nitrous acid) to the bile pigments a play of colour is observed; this is known as Gmelin's test. In the case of bilirubin the colours pass from yellowish-red to green, then to blue, violet, red, and yellow; each of these colours is indicative of a different degree of oxidation of the original bilirubin. Biliverdin gives the same play of colours excepting the initial yellowish-red, which is absent.

Although bilirubin has not been obtained from hæmoglobin, there is no doubt that this is the source of the pigment, for if hæmoglobin be liberated in the blood and enters the plasma, bile pigments appear in the urine; further, hæmoglobin may be readily decomposed, yielding a proteid and hæmatin; and if this hæmatin be deprived of iron, the residue thus obtained is not very dissimilar in composition to bilirubin. We have previously mentioned (p. 11) that old blood-clots contain an iron free substance known as hæmatoidin, and this is practically identical in composition with bilirubin. When red blood cells disintegrate in the ordinary course of their wear and tear, the liberated hæmoglobin is brought to the liver, and under the influence of the liver cells converted into the iron free substance bilirubin or biliverdin. Part of the iron so liberated escapes from the body through the bile, but the bulk of it is retained and again used in the formation of hæmoglobin by the organs which discharge this function.

Though biliverdin is the colouring matter of the bile of herbivora, yet the gall-stones found in the ox consist very largely of bilirubin combined with chalk; in the pig the same combination is observed. Bilirubin is said by Hammarsten to be constantly present in the serum from horse's blood though not in that of the ox, and Salkowski states that it is a normal constituent of the urine of the dog during the summer. In the large intestines both bilirubin and biliverdin undergo reduction resulting in the formation of **stercobilin**, the colouring matter of the fæces in some animals. It is possible also that some of the pigment is reabsorbed from the intestinal canal, carried to the liver, and again eliminated.

The **Bile Salts** are two in number, **glycocholate** and **taurocholate of soda**; they are formed in the liver by the union of **cholalic acid** with **glycine** or **taurine**, and exist in combination with soda. These salts are found in varying proportions in different animals; thus, glycocholate of soda is largely found in herbivora, taurocholate principally in carnivora, while in the pig hyoglycocholic and hyotaurocholic acids are found. Both salts are soluble in water, have a markedly alkaline reaction, rotate the plane of polarized light to the right, and may be obtained in a crystalline form as highly deliquescent acicular needles. Glycocholic acid is the chief bile acid in herbivora, it is produced by the union of glycine with cholalic acid; it is diminished by an animal and increased by a vegetable diet. Taurocholic acid is produced from taurine and cholalic acid and exists principally in carnivora, though small quantities may be found in the ox. This acid differs from the first characteristically by containing sulphur, by which it shows its proteid origin. Glycine or glycocoll also owes its origin to the proteids of the food, and if administered it reappears externally as urea. It cannot be traced in the free state in the body, but occurs in the urine combined with benzoic acid, in the form of hippuric acid. Pettenkofer's test for bile acids is performed as follows: A drop of the fluid is placed on a white earthenware surface, and to it is added a drop of a strong (10 to 20 per cent.) solution of cane-sugar, and a similar quantity of strong sulphuric acid; a beautiful purple-red colour forms. The colour is due to **furfurol**, and is produced by the action of the acids on the sugar and the subsequent reaction with cholalic acid.

The **origin of the bile acids** is involved in obscurity; taurine and glycine are probably formed from the disintegration of proteid, the precursors of cholalic acid are unknown. Nor do we know why glycine should predominate in some animals and taurine in others, but it appears clear that the bile salts are formed in the liver cells. In the intestines a portion of the bile salts is reabsorbed, carried to the liver, and again excreted; or they may be split up in the intestines into their constituents, the glycine and taurine being carried to the liver to be reutilized, while the cholalic acid is excreted. This economical measure has a twofold advantage, for not only can the glycine and taurine be used over and over again, but the bile acids are the best of cholagogues, and stimulate the production of bile.

Bile is secreted under a very low pressure, which is the reverse of what occurs in the saliva; low as the pressure is (·58 inch of mercury), it is higher than that of the blood in the portal vein. If the pressure in the bile duct be raised the bile is reabsorbed, being taken up by the lymphatics of the liver and so conveyed to the blood stream. It is probable that the majority of cases of jaundice are due to obstructive causes, though exceptions to this rule occur. The secretion of bile is a continuous one; whether the animal be in full digestion or fasting, the flow is not intermittent as in the case of the saliva. Though continuous, it is not uniform; it reaches its maximum in the dog between the second and fourth hours after a meal; this is followed by a fall, and again about the seventh hour by a rise. A similar curve is given by the pancreatic secretion, and it can be shown that a specific substance, *secretin*, which stimulates the production of pancreatic juice, also hastens the secretion of bile.

In those animals possessing a gall-bladder this receptacle is filled with bile during abstinence, or if it be empty it is filled even during digestion. The reflux of bile from the biliary duct to the gall-bladder is caused by a sphincter-like contraction of that portion of the duct penetrating the wall of the intestine, by which means the bile is driven back through the cystic duct to the gall-bladder. The bile as formed is propelled along the bile ducts by a contraction of the muscular coat of the tubes, but doubtless both the forcing onward of the bile and the circulation through the liver are largely assisted by the respiratory movements, during which the liver is compressed between the abdominal viscera and the diaphragm.

By some it is considered that no bile enters the bowel while the stomach is empty, but that the passage of acid chyme along the duodenum causes a reflex contraction of the gall-bladder, and an injection of bile into the intestine.

The **amount of bile** secreted varies, but is greater in herbivora than carnivora. Colin's experiments gave him the following amounts as hourly secretions:

Horse	-	8 ozs. to 10 ozs.	per hour		(250 to 310 grammes).
Ox -	-	3 ozs. to 4 ozs.	„	„	(93 to 120 grammes).
Sheep	-	¼ oz. to 5 ozs.	„	„	(8 to 150 grammes).
Pig	-	2 ozs. to 5 ozs.	„	„	(62 to 150 grammes).
Dog	-	¼ oz. to ½ oz.	„	„	(8 to 16 grammes).

The **Use of the Bile** from a digestive point of view is disappointing, inasmuch as it does not digest in the sense that pepsin and trypsin do. It is intimately connected with the function of the pancreas, with which object the secretions are poured out either close together in the bowel, or, as in some animals, by a duct practically common to the two glands. As the horse possesses no gall-bladder the secretion is poured into the intestine as fast as it is prepared; not so with the ox, sheep, pig and dog, where the bulk of it is stored up in a capacious receptacle until required. The reason offered for the horse having no gall-bladder is that as digestion, under ordinary circumstances, never ceases the bile is poured into the bowel as fast as it is secreted, but that in the case of other animals it is only poured out when the contents of the stomach are passing out into the intestine. This explanation, however, does not meet all the difficulties of the case. The following animals, like the horse, have no gall-bladder—the camel, elephant, rhinoceros, tapir, and deer.

The bile being alkaline its first action on the chyme is to neutralize the gastric juice and precipitate the albumoses and peptones. One effect of this is probably to delay the progress of the chyme along the bowel, by which means absorption is assisted.

Bile has a solvent and emulsifying effect on fats, being more active in the presence than in the absence of pancreatic juice. Bile cannot split up fats into fatty acids and glycerine as the pancreas does, but if free fatty acids are present the bile salts are decomposed, their soda set free, and soluble soaps formed; the soaps so formed assist in rendering the emulsifying effect of the bile permanent and the absorption of fat much easier. Fat will not readily pass through a membrane, but if the latter be first moistened with bile the passage is greatly facilitated. In Voit's experiments on dogs it was found that by cutting off the flow of bile to the intestine the absorption of fat fell from 99 per cent. to 40 per cent. The solvent action of bile on fat is the chief digestive function of this fluid, the working constituents being the bile salts. Bile has no action on proteid. According to Hofmeister the bile of the ox, sheep, and horse converts starch into sugar, whilst the bile of the pig and dog possesses no such or only to a limited extent. It has been said that bile has an antiseptic effect on the intestinal contents, keeping them from putrefaction and promoting peristalsis, for it has been found that when it is prevented from entering the bowel, constipation and extreme fœtor of the intestinal contents result. Bile, however, is not a true antiseptic. The clay-coloured fæces obtained in jaundice are probably due to the presence of unacted-on fat; the fat encloses the proteids which putrefy, hence the odour. The bile acts as a natural purgative and keeps up intestinal peristalsis; by so doing it hurries the food out of the system before it undergoes putrefactive decomposition.

Glycogen.

It is quite certain that the largest gland in the body must have some other function than that of the secretion of a fluid of comparatively unimportant digestive power, and such is the case; the liver manufactures and stores up in its cells a peculiar substance known as glycogen or animal starch. Glycogen is spoken of as starch, though it differs from vegetable starch in many important characteristics; thus, it is soluble instead of insoluble in cold water, and it is stained reddish-brown instead of blue by iodine.

The literature of the formation and use of glycogen is extensive, perhaps no substance has given rise to greater controversy; yet the glycogen story which is accepted to-day is the one originally related by Claude Bernard, who was the discoverer of this singular substance.

The sugar in the food, and that derived from starch-conversion, finds its way by means of the intestinal vessels into the portal vein, from here it passes into the liver; under ordinary circumstances it is stored up in the liver as glycogen, being, in fact, reconverted into a kind of starch, and gradually doled out to the system as sugar when required. The liver regulates the amount of sugar which should pass into the blood; so much and no more is admitted to the circulating fluid, the amount varying between ·05 and ·15 per cent. The sugar in the blood of the ox was estimated by C. Bernard at ·17 per cent., in the calf ·1 per cent., and in the horse ·09 per cent. When the liver fails to regulate the amount of sugar in the blood diabetes is produced, and this occurs when the amount of sugar rises to more than ·2 per cent.

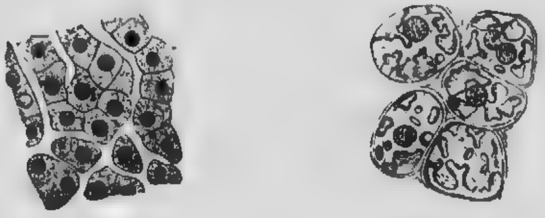
FASTING. AFTER FOOD.

FIG. 56.—LIVER CELLS FROM THE DOG DURING FASTING AND AFTER FOOD (WALLER, AFTER HEIDENHAIN).

During fasting the cells contain no glycogen; after receiving food they become swollen with this substance.

The glycogen which is thus stored up in the liver for future use may in two days be made to disappear by starving and *working* the animal, the material in this way escaping from the liver as sugar, and passing into the general circulation through the hepatic veins. If food, particularly carbo-hydrate, be now given the store of glycogen is rapidly replenished, and the sugar-liberating functions once more established (Fig. 56).

The storing up of glycogen by the liver and its subsequent utilization is very closely allied to a similar process in the vegetable kingdom; the starch in the leaves of plants may pass down the stem as sugar for the purpose of nourishment and be again formed into starch. Similarly in the animal the starch must be first converted into sugar before the bloodvessels of the bowel can take it up, then in the liver once more converted into glycogen, and lastly again into sugar before being finally used by the tissues. The sugar formed from starch in the bowel is maltose, while that formed in the liver from glycogen is glucose. This conversion of glycogen into glucose is due to the presence of a ferment in the liver cells.

The total amount of glycogen obtained from a given quantity of food is not wholly stored in the liver; the latter organ can only hold a limited amount, which in the dog does not exceed 17 per cent. of its weight, and in other animals is less. We know as a fact, that the liver having taken up all the sugar it can from the portal vessels and converted it into stored-up glycogen, allows the balance to pass through the hepatic veins into the general circulation as sugar, and that it is deposited in other organs, principally the muscles, as glycogen for future use. The muscles of well-fed animals contain in this way a considerable quantity of glycogen; even after nine days' starvation in the horse from 1 per cent. to 2·4 per cent. has been found. Ordinarily it may be stated that the muscles hold as much glycogen as the liver, but it takes longer by means of work and starvation to free the muscles from glycogen than to clear the liver.

The presence of glycogen in muscle is not essential to contraction, for there are muscles in which no glycogen is found and yet in which active contraction takes place. In the muscles of the embryo, before striation has occurred, the amount of glycogen existing is something considerable; as much as 40 per cent. of the dry material of the embryo muscle may consist of this substance. As striation appears the glycogen leaves the muscles to a great extent, and the liver takes on the process of production.

The Use of Glycogen.—The existence of glycogen in the embryonic muscle points to its use in active nutrition and rapid growth; further, it is found in the placenta, where it is used for the nourishment of the fœtus, and also in rapidly developing cells, such as some found in cartilage and the white cells of the blood; in all these and other places it is simply stored for future requirements. In the adult the chief use of glycogen is to facilitate the metabolic production of muscular energy and animal heat, and this it does in its glucose form as the result of oxidation.

The **sources of glycogen** have been a fertile cause of discussion and object of experimental inquiry. It was natural to consider, as we have so far done, carbo-hydrate material as the chief contributing agent; it was less certain whether proteids contributed, while the consensus of opinion was against fat taking any share in the process. We must examine each of these in a little more detail.

We have learnt that starch is not absorbed as starch, but, depending upon the nature of the diastatic ferment, is converted into maltose, or maltose and some dextrin, and subsequently dextrose. These sugars are readily converted into glycogen by the liver cells by the process of dehydration. Cane-sugar and milk-sugar are not readily converted into glycogen, but since these double sugars undergo inversion in the intestinal canal before absorption—cane-sugar into dextrose and levulose, and milk-sugar into dextrose and galactose—they may in this form be readily converted into glycogen. The effect of proteid on glycogen formation is not so easily settled. It is observed that in diabetes, though all carbohydrate food be withheld, yet sugar may appear in the urine on an exclusively proteid diet; the same thing is observed in the experimental glycosuria which may be produced by the administration of phloridzin, and, furthermore, that sugar may be produced even when the animal is starved. The conclusion appears irresistible that proteid can produce sugar, and this is explained by saying that certain proteids split into a nitrogenous and non-nitrogenous portion, the former being converted into urea, while the non-nitrogenous residue is converted into sugar and may thus give rise to glycogen. Proteids, such as casein, which do not contain a carbo-hydrate group, may take no share in the production of glycogen. There are a few observers who regard fat as a source of glycogen, and there is some evidence to show that it may contribute, for it has been said that glycerin acts as a sugar former. If this is so the conversion of fat into glycogen through its splitting up in the intestinal canal into fatty acid and glycerin would not be a difficult matter. On the other hand, experiment shows that when an animal is fed solely on fat, the glycogen disappears from the liver as quickly as it does in starvation. The question is, therefore, very far from being settled.

The Liver Ferment.—When a liver is rapidly removed from the body of a recently killed animal which has been appropriately fed, it contains a quantity of glycogen; if it is allowed to stand the glycogen gradually becomes reduced in amount and sugar takes its place; finally all the glycogen disappears. This change is brought about by a diastatic ferment in the liver cells which changes the glycogen into sugar. If the liver on removal from the body be rapidly minced and boiled, the ferment is destroyed and dextrose is not formed.

How the Supply of Sugar is Regulated.—Glycogen is a temporary reserve of carbo-hydrate material, which is issued as required to the system in the form of glucose, and by the process of oxidation yields heat and energy. It is readily used up in the interval between meals and readily renewed. The sugar in the blood maintains a remarkably regular percentage, ·1 to ·2 per cent., and no doubt this is effected by the gradual supply of this material from the temporary reserve stored in the form of glycogen. Should the percentage of sugar rise in the blood, the excess is got rid of through the kidneys (diabetes) and lost to the body. The liver itself does not appear to be able to regulate its sugar output to the blood; this would seem to be one function of the pancreas, the ‘internal secretion’ of which, in some way which is not clearly understood, prevents the liver giving off its glycogen as sugar too rapidly. Removal of the pancreas, as we shall show later, is followed by diabetes. If expressed pancreatic and expressed muscle juice be mixed together an active glycolytic substance results, and it is considered that as neither of the above are capable of acting alone, the internal ferment of the pancreas acts upon a ferment in the muscles and makes the decomposition of sugar possible.

Diabetic Puncture.—Bernard discovered that if the floor of the fourth ventricle be punctured at a certain definite spot, temporary diabetes resulted, the urine contained sugar, and the liver possessed no glycogen. This spot is known as the diabetic centre, and the effect of the puncture is to stimulate it and temporarily destroy the glycogen-holding capacity of the liver, in consequence of which the material is liberated as sugar. The evidence of this is that if the animal be starved before the puncture is made no sugar appears in the urine. Stimulation of the central end of the vagus or of the depressor nerve produces glycosuria, though stimulation of the first causes the abdominal blood-pressure to rise, and of the second causes it to fall. From this circumstance it is considered that the effect of the puncture is not to produce mere vascular dilatation, but rather that it stimulates some secretory nerve. The diabetic centre is a reflex one, the afferent or ingoing nerves being most of the sensory nerves, the efferent being the spinal cord, sympathetic and splanchnics. It has been suggested that the muscles at the moment of contraction set up afferent impulses which are carried to the diabetic centre and sugar thus liberated. This would place the muscle in the position of not only using up sugar but of being able to call forth its production as required. If this be proved to be true, it is easy to understand how the heart, the most active muscle in the body, is able to regulate the production of its energy yielding substance.

Further Uses of the Liver.

We have studied two uses of the liver, viz., the formation of bile and the storing up of glycogen, but there are other functions of this gland to consider.

Another important use of the liver is the formation of urea. The source of urea is the proteid constituent of the food, which in the process of disintegration yields certain amido-acids such as leucine and tyrosine. These substances may be formed in the intestinal canal as the result of pancreatic digestion, or they may be formed in the living cell as the result of the breaking down of proteid. Under any circumstances the leucine undergoes a series of oxidative changes, mainly in the liver, resulting in the formation of urea which is passed on to the kidneys for excretion.

The further facts regarding the formation of urea are best dealt with in the section devoted to the kidneys.

As the result of proteid decomposition in the intestinal canal certain aromatic compounds are formed; these are united with sulphuric acid and got rid of by the kidneys as conjugated sulphuric acids. In this combination the originally *poisonous proteid products* are converted into non-poisonous ones, and this change is effected in the liver (Bunge). In this we have a very important function of the liver demonstrated, viz., as a neutraliser of poisons introduced into the blood by the intestines. It is a noteworthy fact that many metallic poisons are also arrested in the liver, for example mercury and arsenic.

The numerous and complicated changes produced by the liver may thus be summarized: It forms bile, regulates the supply of sugar to the system, and stores up as glycogen what is not required. It guards the systemic circulation against the introduction of certain nitrogenous poisons, such as ammonia, by transforming them into urea, and against other poisons of proteid origin by converting them into harmless products, by conjugation with alkaline sulphates.

Section 2.

The Pancreas.

The fluid secreted by the pancreas performs certain important functions in digestion. It has been remarked that there is scarcely any animal which does not possess a secretion allied to the pancreatic; even those invertebrates without a peptic or biliary apparatus are in possession of one. From the resemblance of the pancreas to the salivary glands, it has been termed the abdominal salivary gland.

The pancreatic fluid from herbivora can only be obtained with extreme difficulty; to establish a pancreatic fistula in the horse is a formidable operation, necessitating an incision from the sternum to the pubis and the turning back of the bowels. Colin has established these fistulæ both in the horse and ox, but the profound impression on the nervous system produced by such extensive interference must considerably affect the character of the secretion and the amount manufactured.

Pancreatic fluid is an alkaline, clear, colourless fluid like water, and though viscid in some animals is not so in the horse. It has a saltish unpleasant taste, and a specific gravity of about 1010; the viscid secretion of the dog has a specific gravity of 1030. The following analysis of the fluid in the horse is given by Hoppe-Seyler:

Water	98·25		
Solids	1·74	Organic matter	·88, containing ·86 of ferments.
		Salts	·86, „ much sodium phosphate.
	100·00		

Schmidt found the fluid of the dog to have the following composition:

Water	90·00		
Solids	9·92	Organic matter	9·04
		Salts	·88 containing much sodium chloride.

The salts present are sodium chloride in abundance, potassium chloride in traces, sodium carbonate and phosphate, calcium and magnesium phosphates in small quantities. The organic solids are remarkable for the amount of proteid present in them; they vary in amount in different animals, for example 9 per cent. in the dog and ·9 per cent. in the horse.

Mechanism of Pancreatic Secretion.—The pancreatic secretion is influenced by special secretory nerves; stimulation of the vagus or splanchnic may, after a long latent period, give rise to a secretion, though it is not yet settled whether these fibres produce it during the act of digestion. The outpouring of the acid chyme from the stomach into the duodenum at once gives rise to a secretion of pancreatic juice, and it was supposed that the acid acted on the secretory nerves and produced a secretion reflexly. Bayliss and Starling, however, demonstrated the remarkable fact that if an extract of the mucous membrane of the duodenum or jejunum be made by scraping the bowel, and acting on it by weak hydrochloric acid, a substance may be obtained which when injected into the blood produces a profuse pancreatic secretion. To this internal secretion of the intestinal cells they gave the name **Secretin**, the nature of which has not been determined. Two facts are clearly established, first, that it is not a ferment as it is not destroyed by boiling, and secondly that acid is an essential part of the process, for if the mucous membrane of the bowel be extracted with either water or saline solution secretin is not obtained. It is the *acid* chyme, therefore, acting on the mucous membrane of the intestine which produces secretin; this is absorbed by the blood, and thus produces its specific action on the pancreas.

Uses of the Secretion.—The pancreatic juice is poured into the bowel in the horse and sheep by an opening common to the pancreas and liver, while in the ox, pig, and dog, the ducts of the liver and pancreas are separate, and open within a short distance of each other.

It is essentially a digestive fluid, and acts on the three classes of food stuffs, viz., proteids, fats and carbohydrates; to enable this to be effected, it contains three ferments or their precursors, viz.:

A Proteolytic Enzyme which acts on proteids (*Trypsin*).
A Diastatic Enzyme which acts on carbo-hydrates (*Amylopsin*).
A Lipolytic Enzyme which acts on fats (*Lipase or Steapsin*).

Observations appear to show that the proportion of each of these ferments in the secretion depends on the character of the food; if, for example, the food is rich in fat the secretion would be rich in lipase. It is also probable that not only does the nature of the food determine the predominance of each enzyme, but also the amount of fluid to be secreted. This, as a rule, reaches its maximum in the dog between the second and fourth hour after taking food, and corresponds to the greatest activity of the liver. In dogs which have been starved active secretion of bile, pancreatic juice, and intestinal fluid, takes place, it is said, every two hours, and lasts for twenty minutes. The cause of this is by no means clear. All the fluid thus poured out is reabsorbed.

Trypsin.—It has been observed that pancreatic juice taken direct from a fistula in the duct may have little or no action on the proteids of food, but if the same fluid be allowed to become contaminated by the intestinal contents it at once becomes active. Evidently the addition of a something from the bowel has brought about a marked change in the proteolytic character of the secretion. Investigation shows that though the secretion taken direct from the pancreas contains the precursor of trypsin, viz., **trypsinogen**, yet in the latter form the ferment is unable to act on the proteid of food until it has itself been acted upon by another ferment. This ferment is derived from the mucous membrane of the intestinal canal. A ferment acting on a ferment has been described as a **kinase**, and as this one is derived from the bowel it is called **enterokinase**, a very small amount of which is capable of converting inactive trypsinogen into active trypsin. It is remarkable that of the three ferments secreted by the pancreas, trypsin is the only one which is secreted in an inactive condition. Pawlow considers this to be due to the fact that if trypsin were active *in* the pancreatic juice, it would destroy its fellow-ferments, but that in the bowel these ferments are protected.

The fact that extracts of pancreas, as obtained usually from a slaughter-house, may be made more tryptically active by the addition of a little dilute acetic acid, does not now imply that the acid has converted the trypsinogen into trypsin, as has usually been supposed. The pancreas used in the preparation of the extracts is already contaminated with minute quantities of enterokinase, whose activity is greatly increased by neutralizing the alkalinity of the extracts. If a pancreas be obtained under conditions which ensure the absence of any admixture with even traces of enterokinase, extracts of such a pancreas cannot be rendered more tryptically active by the addition of dilute acid (Starling).

It is here desirable to draw attention to the fact that secretin and enterokinase are both derived from the mucous membrane of the intestinal canal, and care must be taken to avoid confusing them: the former is not a ferment, the latter is. The function of secretin is to cause the production of pancreatic juice, that of enterokinase is to endow one of the ferments of the pancreatic juice with its remarkable proteolytic properties.

The action of trypsin on proteids is most interesting. The proteid molecule is very complex; the use of trypsin is to split it up into simpler products, with the object of facilitating its absorption. As we shall point out later, no food substance is taken up excepting in its simpler form, and the proteids of oats, barley, hay, or flesh, have to be reconstructed in order to form part of the tissues of the living animal. To enable this to be done trypsin acts on the large proteid molecule and breaks it down in the production of a number of simpler bodies of smaller molecular weight; on these the tissue cells set to work, and by a process of synthesis construct the form of proteid needed by the body. It can be easily shown that the action of trypsin on proteid is much more satisfactory and thorough if the latter has previously been acted upon by pepsin. Trypsin like pepsin produces albumose and peptones; but the process does not stop at peptone, no peptone can be found in the blood, and none remains after a prolonged pancreatic digestion. The action of the trypsin is, in fact, to produce a large number of simpler end-products, of which the amido-acids leucine and tyrosine are the best known and most easily obtained: besides these aspartic and glutaminic acids, tryptophan, and the hexone bases lysine, arginine, and histidine. Should any proteid or peptone have escaped the action of pepsin and trypsin, it may be attacked by another enzyme found in the intestinal mucous membrane, known as **erepsin**, which also has the power of breaking down albumoses and peptones into leucine and tyrosine. Erepsin is found in most of the tissues of the body, so is not specific to the intestine.

Under the influence of bacterial action aromatic bodies are formed—phenol, indol, and skatol, the latter being responsible for the fæcal odour of a pancreatic digestion mixture. These substances are produced from tryptophan, one of the end products of the primary decomposition of proteids.

Amylopsin, the diastatic ferment, has an action on starchy food similar to that of ptyalin, but more rapid, the final products being maltose and achroodextrin. The hydrolytic action of amylopsin stops at maltose and achroodextrine, but these are in turn attacked by the **maltase** of the succus entericus and converted into dextrose.

Lipase or **steapsin**, the fat-splitting ferment, acts upon neutral fats, splitting them into free fatty acid and glycerin. The splitting process is followed by saponification, viz., the liberated fatty acid combines with the alkaline salts to form soaps; as the result of this the production of an emulsion becomes possible. In emulsification the oil globules are rendered extremely small without the power of coalescing, and at one time it was considered that fat in this finely divided state was capable of entering the villi, but there can be no doubt that the minute fat globules are further split into fatty acid and glycerin, and that only the products of this splitting enter the villi. Once, however, within the epithelial cells of the villi, the synthesis of fatty acid and glycerin into fat becomes possible, and recent work indicates that this may be effected by lipase; in other words, the same ferment which does the splitting is possessed of a reversible action. Lipase is readily destroyed, so that unless quite fresh it does not work in artificial digestions. Under natural conditions it is greatly aided, and the process rendered much quicker by the action of the bile.

On p. 170 we have alluded to Pawlow's work on the quantity and quality of the gastric juice, being regulated by a specific action on the part of the food itself. Similarly, the same observer has shown that the ferment contents of the pancreatic juice are adapted to the character of the diet; a definite and constant diet leads to the formation of a pancreatic juice which is unable to deal effectively with a sudden change in diet. The practical bearing of this in the feeding of animals is far-reaching. As a profession we have recognised for years the disastrous effects of sudden changes in diet; modern science offers the explanation of its action, which in all probability is brought about as the result of an internal secretion.

The **Changes occurring in the Cells** of the gland correspond very closely with those described for the salivary secretion.

When a pancreas or lobe of a pancreas has been at rest for some time the cells forming it are rendered very indistinct; the lumen of the alveolus is nearly obliterated by their swollen condition, and the cells are seen crowded with granules; these are so arranged that the margin presents a clear or fairly clear zone, while within this there is an intensely granular zone (Fig. 57, A). The minute granules filling the cell are the mother substance of the secretion. When activity commences the granules appear to pass centrally towards the alveolus, leaving the cell comparatively clear excepting that portion immediately abutting on the alveolus, which even in the exhausted condition remains granular. These changes result in the cells becoming distinct and clearly defined, and moreover, as they have emptied their granular contents into the alveolus as pancreatic secretion, they have consequently become much smaller. The narrow clear zone seen in the resting gland has now become broad, the previously choked alveolus is readily defined, whilst the nucleus of the cell, which was hidden in the charged condition, can easily be seen in the exhausted gland (Fig. 57, B). These changes have been worked out on the pancreas of the living rabbit by Kühne and Sheridan Lea.

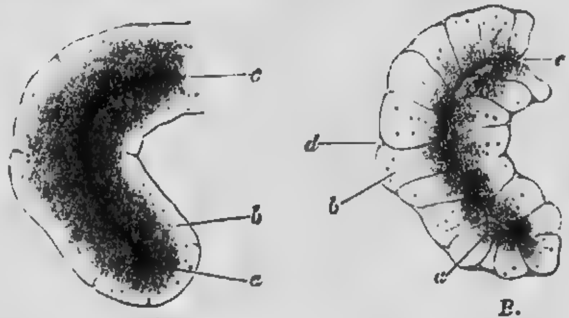

FIG. 57.—A PORTION OF THE PANCREAS OF THE RABBIT (KÜHNE AND SHERIDAN LEA). A, AT REST; B, IN A STATE OF ACTIVITY (FOSTER).

a, The inner granular zone in A is larger and more closely studded with fine granules than in B, in which the granules are fewer and coarser. *b*, The outer transparent zone is small in A, larger in B, and in the latter marked with faint striæ. *c*, The lumen is very obvious in B, but indistinct in A. *d*, An indentation of the junctions of the cells seen in the active but not in the resting glands.

Amount of Secretion.—From the investigations of Colin and others we know that in most animals the secretion of pancreatic juice is continuous though not uniform. In ruminants the largest secretion is towards the end of rumination; in the dog the maximum is reached between the second and fourth hours after feeding, this maximum being followed by a fall, and about the seventh hour by a rise. It will be remembered that the bile gives a similar curve. In the dog it is generally considered there is no secretion during starvation, but immediately food begins to pass out of the stomach the pancreas becomes active. In this connection, however, it is desirable to remember that according to some observers a starved dog will actively secrete pancreatic juice for twenty minutes every two hours. The continuous secretion of the gland in herbivora is provided for by all the lobes not being active at the same time. In the ox the amount of juice secreted is between 7 and 9 ozs. (265 grammes) per hour, in the horse it is much the same, in the sheep ¼ to ½ oz. (7 to 8 grammes), pig about ⅛ to ½ oz. (5 to 15 grammes) per hour, and in the dog still less (2 to 3 grammes). There is no necessary ratio between the size of the animal, the weight of the gland, and the amount of pancreatic fluid secreted; carnivora secrete relatively more than herbivora.

The pressure under which the pancreatic juice is secreted is low; it is said to be equal to ·67 inch of mercury, which is very little greater than that of the bile.

Pancreatic Diabetes.*—If the pancreas of a dog be completely removed there is a disappearance of all glycogen from the tissues, and the animal dies in the course of a month or less with diabetes, since the power of oxidizing glucose is lost. The glucose consequently accumulates in the blood, and is separated by the kidneys. In addition to there being sugar in the urine, there is also an increase in the amount of fluid produced and an excess of urea. If the depancreated animal be placed on a purely proteid diet, no difference occurs in the amount of sugar excreted; even if no food be given sugar is still formed. If the removal of the gland is incomplete glycosuria still occurs, but it will vary in intensity from fatal to transient effects, depending upon the amount of pancreas left behind, and this is explained by the fact that sugar may be formed from proteid. In fact, it is possible by experience to leave behind just sufficient of the gland to prevent diabetes arising. In any case fatal results may be avoided by grafting portions of pancreas beneath the skin, the presence of these preventing diabetes.

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* To avoid repetition, this matter should be read in conjunction with the remarks on Glycogen, p. 229.

Evidently, therefore, in some way pancreatic tissue is intimately mixed up with the sugar question, and it has been assumed that the pancreas produces an 'internal secretion' (see p. 229), the use of which is devoted to preserving the organism from an excess of sugar, either by regulating the amount which is to be liberated into the blood from the seats of sugar production (liver and muscles), or by stimulating the sugar-splitting action of the tissue cells (p. 230). Very little is known of the subject; it certainly appears that the acting agent is not an enzyme, for its property is not lost in a pancreas which has been boiled; further, the internal secretion cannot act alone, it requires the presence of a ferment formed in the muscle, and the combination is then capable of rapidly decomposing dextrose.

The blood, as pointed out previously (p. 226), will not tolerate more than ·2 per cent. of sugar in circulation, anything over this is rejected and got rid of through the kidneys; in pancreatic diabetes there may be double this amount of sugar in the blood.

Histologically, the pancreas is a compound tubular gland like the salivary glands, but there are certain groups of cells peculiar to it which form spherical or oval bodies capable of being seen with the unaided eye. These are known as the *Islands of Langerhans;* each is surrounded by a rich capillary network of bloodvessels, and the view has been advanced that these islands are the seat of the internal secretion of the pancreas.

Pathological.

The most common pathological condition of the liver is **Jaundice**, and the majority, if not all, cases of jaundice are obstructive, viz., there is some obstruction to the free pouring out of bile; in consequence there is a backward pressure, which being greater than the low blood-pressure under which bile is secreted, the bile is reabsorbed, and stains the tissues yellow. There is also a form of jaundice affecting the horse and dog in South Africa, due to a parasite in the blood, but in these cases the yellow tint is derived from the destruction of red corpuscles and the liberation of their colouring matter. **Biliary Calculi**, consisting largely of cholesterin, are not uncommon in ruminants, but rare in the horse. **Fatty Liver** is common in all animals over-fed and under-worked. In the horse it may lead to **Rupture** of the liver during work. **Enlargements** of the liver are very common as the result of vascular disturbance elsewhere; it is not uncommon as a sequel to pneumonia, strangles, and other prolonged febrile changes. **Abscess** of the liver is rare, but not unknown. **Parasitic** disease of the liver is one of the epizootic diseases of sheep, and common in the ox, but rare in the horse. The parasite occupies the bile ducts, which become practically occluded.

In India, calcareous degeneration of the liver is one of the most common affections of this organ, and throughout the tropics generally liver disorders are very frequent.

The pancreas is seldom the seat of pathological disturbances; it may be affected with abscess in strangles or in septic diseases, but such conditions are unrecognisable during life.

CHAPTER VII

ABSORPTION

Section 1.

Lymph.

Lymph may be regarded as the material by which the tissues are directly nourished, and by which effete material is collected from them and taken back to the blood; there are certain non-vascular structures, such as the cornea, cartilage, etc., where the lymph circulation is the only means by which the part is supplied with nourishment. Speaking generally, however, the lymphatic system may be described as the drainage system of the body, in contradistinction to the blood or irrigating system.

The Lymph Spaces.—The tissues are bathed in lymph, which is contained in the lymphatic spaces existing between the capillary blood-vessels and capillary lymph-vessels. There is a constant passage of material from the blood into the tissues, and from the tissues into the blood.

The lymph spaces are irregular passages in the connective tissue, the larger ones being lined by epithelioid plates of a peculiar irregular outline; these spaces exist outside the bloodvessels, and the lymph finds its way from the bloodvessels into the lymph spaces. From the lymph spaces the fluid reaches the lymph capillaries, but the means by which it gets there is not clear, for it appears certain that excepting in a few cases there is no direct communication between the space and the capillary. In the vessels of the brain a peculiar arrangement is present. the lymphatic vessel surrounds the artery and obtains its lymph direct; such are known as peri-vascular lymphatics. The lining of the **Lymph Capillary** is composed of the same epithelioid plates with irregular outline which are found in the spaces, and it is believed that at the junction of the plates, crevices or intervals may exist through which fluid may find its way by the simple process of transudation. From the lymph capillary begins the **Lymphatic Vessel**, which in addition to an epithelioid lining has also a muscular coat, more marked in the large than in the small vessels, and also a connective-tissue covering. In the interior of these vessels valves are found which are essentially similar in structure, arrangement, and mode of action to those in the veins. Immediately beyond each valve there is a dilatation of the vessels which gives them a beaded appearance when the lymphatic is distended.

The whole of the lymphatics of the body converge towards a central vessel, the thoracic duct; those from the left side of the head and neck, the left fore limb, the chest, abdominal cavity, and hind limbs, unite with the duct at different points, and this in turn opens into the anterior vena cava; from the right side of the head and neck, and right fore limb, the vessels collect and pour their contents by a separate duct into the same vein. The thoracic duct is nothing more than a large lymphatic vessel, possessing the same structure as the lymphatic vessels above described, the muscular coat being especially well marked. The thoracic duct receives the lymph not only from the ordinary tissues but also from the intestinal canal. During starvation the mesenteric lacteal vessels convey to the duct a fluid which is essentially lymph, but during digestion this clear fluid is replaced by a turbid white fluid known as chyle; at this period the lacteal vessels are carrying not only lymph but also the products of digestion, the milkiness of the chyle being due to the presence of emulsified fats.

The **Serous Cavities** of the pleura, pericardium, and peritoneum, have been looked upon as large lymphatic spaces, though even this is now by some considered doubtful. The fluid they contain is lymph, and they are in direct communication with lymphatic vessels, especially those of the diaphragm. In the diaphragm slits or stomata exist, and into these the lymph readily finds its way, being aspirated into the vessels during the respiratory movements of this organ; so readily is this effected that the diaphragm may be injected in a recently dead subject, by placing some milk on its surface and establishing artificial respiration.

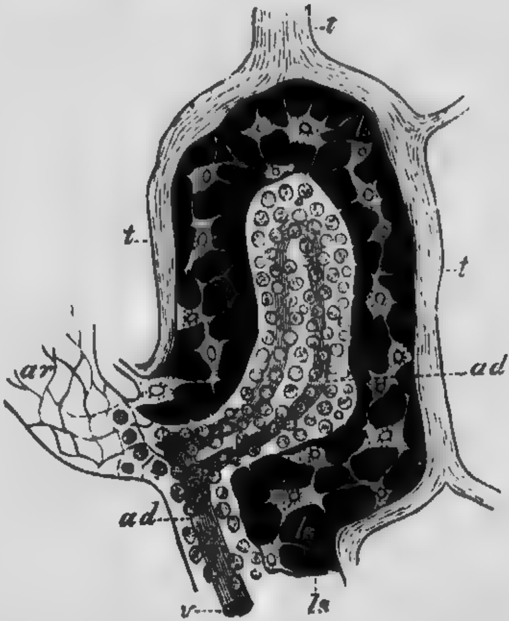


Fig. 58.—Diagrammatic Section of Lymphatic Gland.

ad, Adenoid tissue containing lymph corpuscles, excepting to the left of the figure *ar*, where they are omitted in order to show the adenoid reticulum. The region *ad* is normally densely packed with lymph corpuscles and constitutes the glandular substance. The corpuscles are here drawn in scanty numbers, so as not to obscure the central capillary *v*. In the adenoid tissue may be seen a capillary blood-vessel *v*. Outside the core of adenoid tissue is the lymph sinus or space *ls*, across which run branched nucleated corpuscles which are simply an open network of connective tissue. These corpuscles are shown on a black ground in order the better to distinguish the lymph space. Surrounding the whole is the trabecular framework *t*.

The lymphatic vessels in their course pass through bodies known as **lymphatic glands**, entering at one side and emerging at the other. Experience shows that in its passage through these glands the lymph has corpuscles added to it which ultimately become white blood corpuscles, and moreover it acquires the property of clotting. The gland consists of a *capsule* within which is a mass of adenoid tissue divisible into a *cortex* and *medulla*. The capsule sends in bands of tissue (*trabeculæ*) which divide the gland into compartments or *alveoli*, those in the cortex being much larger than those in the medulla. The alveoli contain a network of connective tissue whose central part is finely meshed (*adenoid tissue*), closely packed with lymph corpuscles and constitutes the *glandular substance*. The adenoid tissue does not occupy the entire alveolus, but fills up the centre, and is maintained in position by branched, nucleated, connective tissue corpuscles passing to the wall of the alveolus. In this way a space or channel is formed between the central mass of adenoid tissue and the wall of the alveolus; this channel is known as a *lymph-sinus* (see Fig. 58). It is through the lymph-sinuses of the cortex that the gland is in direct communication with the afferent lymphatic vessels. In the adenoid tissue of the alveolus is found a network of bloodvessels; the tissue itself is filled with corpuscles known as leucocytes, which are also found in the more open network extending across the lymph sinus. The medulla of the gland presents no essential difference in structure to that of the cortex, excepting that the reticular network is more complex, closer, and more extensive. The efferent lymphatic vessels originate in the lymph sinuses of the medulla.

Lymph is a slightly yellow-coloured fluid, alkaline in reaction, with a specific gravity of 1012 to 1022, and possessing the power of spontaneous clotting. The clot it yields is not so firm as that of blood and takes longer to form; moreover, the bulk of fibrin is much smaller. Lymph may be regarded essentially as blood minus the red corpuscles; it contains, therefore, the proteids of that fluid, viz., fibrinogen, paraglobulin, and serum albumin though in smaller amounts, cells resembling the white cells of the blood, extractives, salts, and gases. The fluid in which these are contained is spoken of as lymph plasma. The gases consist principally of carbon dioxide, whose amount is greater than in arterial but less than in venous blood, a small quantity of nitrogen, and only traces of oxygen. Amongst the extractives some observers have found urea, a substance which exists more largely in lymph than in blood, and which is said to be always present in the cow. The salts are distributed much as are those in blood, viz., potash and phosphates in the corpuscles, and soda in the plasma. It is evident that the composition of the lymph cannot be uniform but must depend, among other causes, upon the nature of the food supply, and the source of the lymph.

The lymph cells or leucocytes exhibit amœboid movements and are identical with white blood-cells; they are more numerous in those vessels which have passed through lymphatic glands, for it is in the gland that the leucocytes are manufactured and added to the lymph. The cells consist of proteids, lecithin, cholesterin and fat, and their nuclei contain nuclein. Owing to their power of movement they are able to pass through the bloodvessels into the tissues and *vice versa.* The proportion of lymph corpuscles to fluid is about the same as the proportion of white corpuscles to blood.

The **Quantity of Lymph** in the body is difficult to arrive at, and varies considerably. Colin obtained from a lymphatic in the neck of horses between 1 to 4 lbs. (½ to 2 kilos) in 24 hours; the mean amount was 2 lbs. 6 ozs. (2 kilos) for the same period, but he notes that the variations are very wide, and that herbivora secrete more than carnivora, and young animals more than adults. The amount of material collected from the thoracic duct of a cow in 24 hours has been found to be 209 lbs. (91 kilos), but this is no guide to the quantity of lymph in the body, as the material in the thoracic duct is mixed with the chyle from the intestines. It is usual, however, in this vessel to consider two-thirds of the contents to represent chyle and one-third lymph. The quantity of mixed chyle and lymph obtained by Colin from the thoracic duct, some hours after the animals had been fed, was as follows:

Horse, 80 to 90 lbs. (14 to 40 kilos) in 24 hours.
Ox, 46 to 209 lbs. (20 to 91 kilos) " "
Sheep, 6½ to 10 lbs. (3 to 9·5 kilos) " "
Dog, 3 to 6 lbs. (1·3 to 2·6 kilos) " "

The Formation of Lymph.—The theory of lymph formation is by no means settled; the rival views may be classified as physical and secretory. The physical theory is based upon the laws of filtration, diffusion, and osmosis, while the secretory or vital theory is based upon the activity of the living cells of the body. The *physical* theory will first claim our attention, and it is the one which at the present time finds, perhaps, more general acceptance. According to this theory lymph is formed as the result of the operation of the three following factors.

Filtration through the walls of the capillaries from the blood to the tissues is always possible when the pressure of blood in the capillaries is higher than that of the fluid in the tissues. It can easily be shown that an increase or decrease in capillary pressure increases or decreases the amount of filtration.

Diffusion and Osmosis.—The difference existing between the composition of the blood plasma and the liquid in the tissues outside the capillary vessel is a cause of diffusion and osmosis. Such differences are frequent, as for example, after every period of digestion, and the equilibrium of composition can easily be restored by the setting in of diffusion and osmotic currents. Differences in composition may arise not only between the blood and the tissues but the tissues and the blood, and in both cases are adjusted in the same way. Diffusion in liquids seems, as in gases, to be the result of the continual movement of its molecules, so that two liquids miscible, but utterly unlike, if brought into contact will gradually form a homogeneous mixture; or if they be separated by a membrane permeable to the molecules, diffusion will occur through this and a mixture of uniform composition result. Diffusion through a membrane is known as osmosis. Substances which are diffusible are known as crystalloids, those which are non-diffusible are called colloids. Sugar or salt are good examples of diffusible bodies, proteid and starch are examples of colloids, the large size of the molecules of the latter preventing their passage through an animal- or other membrane. This difference in the behaviour of these two classes of substances as regards their osmotic properties affords a useful and ready means known as *dialysis* of separating the crystalloids from the colloids.

If two masses of water be separated by a membrane the diffusibility of each being equal, as many molecules will pass into one chamber as enter into the opposite, though to all appearances no change in the fluid is taking place. If one chamber contains salt solution and the other plain water, it will be found that much more water passes into the salt solution than salt solution into the water, the rate of transference of the salt depending upon the concentration of the salt solution; the force which brings this about is known as the *osmotic pressure*. It can be shown that the osmotic pressure is proportional to the number of molecules of the crystalloid in solution.

If a strong solution of common salt be injected into the blood, an osmotic current is created proceeding at first from the tissues into the blood; in course of time the salt will diffuse out of the vessels into the tissues and an osmotic current will then be set up in an opposite direction, viz., from blood to tissues. The diffusibility of proteid substances is very slight or entirely absent, their osmotic properties are correspondingly small and by some have been denied. It is therefore difficult to explain the passage of the proteids from the blood to the tissues, excepting on the ground of filtration.

A picture of what is occurring in the tissues under ordinary functional activity is probably as follows: The tissue elements are nourished by the lymph thereby effecting an alteration in the composition of the latter, which is made good by diffusion and osmosis from the blood. As the result of tissue activity the proteid molecule gets broken down with the production of simpler and crystalloid bodies. These pass into the lymph from the tissues, and raise its concentration; by so doing they draw water from the blood-vessels to the lymph, or if the concentration in the latter is less than that of the blood, diffusion occurs from lymph to blood.

The permeability of the capillary wall as a factor in lymph production has been treated by Starling. He finds that whereas the capillaries in the limbs and connective tissues generally present a very considerable resistance to the filtration of lymph through them, and keep back a large portion of the proteids of the blood-plasma, the intestinal capillaries on the other hand, are much more permeable, while those of the liver are of the greatest permeability, a very small capillary pressure producing a large transudation of lymph containing as much proteid as the plasma itself. So slight is the effect of capillary pressure on lymph production in the limbs and connective tissues, that in other parts of the body it has been necessary to explain the production as mainly due to diffusion and osmosis. Constant osmotic interchange between blood and tissue-cell occurs through the medium of the lymph, and with remarkable rapidity; thus, if the osmotic equilibrium be disturbed by injecting a large dose of dextrose into the circulation, within half a minute it is readjusted. The slight influence of capillary pressure in lymph production, mentioned above, only holds good for the normal capillary; any impaired nutrition of the vascular wall, which may easily arise, increases its permeability, and the slightest increase of capillary pressure then produces an increase in lymph production.

Starling records the remarkable fact that no lymph can be obtained from a *resting* limb, though active or passive movements of it at once cause a flow of lymph. The only part of the body which produces a continuous flow of lymph during rest is the alimentary canal. Though no lymph is yielded by a resting limb, yet the chemical changes in the tissue are still occurring, oxygen is being absorbed, carbonic acid and other waste products got rid of, but their channel of excretion is effected by the blood-vessels.

The *secretory* theory of lymph production is based on the knowledge of the secretory activity of epithelium generally. It was natural, therefore, to regard the endothelial lining of the capillary vessels as the possible seat of secretory activity. Heidenhain, the exponent of this theory, showed that certain bodies (*Lymphagogues*) when injected into the blood-stream caused an increased flow of lymph, and he regarded these as direct excitants of secretion. The opponents of this theory show that these substances act by their deleterious effect on the capillary wall, or by their causing water to be taken up from the tissues; the effect of taking up water is to raise the total volume of blood in the vessels, and so cause a general rise in blood-pressure, and in consequence a transudation of lymph.

At present it is not possible to decide between the rival theories of lymph formation; it may be proved that under given conditions both play a part in the process. It seems impossible to exclude the living activity of the cell-body, so strongly urged in the matter of other secretions, while it is equally certain that there are other conditions which are only possible of explanation on a physical basis. We cannot suppose that the condition of the cells forming the capillary wall is invariably the same. This wall is the membrane across which the physical factors have to play their part. Even if the latter are the chief agents in the whole process they must still be more or less subject to the changing states of the cellular capillary wall. And in connection with both these views, it is well to bear in mind that no lymph-secretory fibres have been discovered, though their existence is possible, and further we do not know positively in which way the tissue spaces communicate with the lymphatic vessels, or whether, like the blood-vessels, the latter form a closed system.

As fast as the lymph finds its way into the spaces it is normally passed on to the lymphatic capillaries, so that the rate of output is equivalent to the rate of removal; when however the output is greater than the rate of removal the lymph accumulates in the tissues and **Œdema** results. It is conceivable that the rate of removal need not necessarily always be at fault, but that the rate of secretion may be so greatly increased that the outgoing channels are unequal to the demands made upon them. Such an increased secretion of lymph lies on the shoulders of the vascular system, and experience shows that in the majority of cases increased formation of lymph is a more common cause of œdema than defective drainage. It is well known that interference with the venous circulation is productive of œdema; disease of the right side of the heart or portal obstruction is a fruitful source of trouble, the explanation being that there is not only an increase of pressure in the capillaries as the result of the venous obstruction, but also a back flow of venous blood which is kept in contact with the wall of the capillary, and induces changes in the epithelioid cells resulting in increased lymph formation. The swollen legs so common in horses kept idle in the stable are practically due to the same cause. The venous blood ascends the limbs against gravity and exerts on the capillaries of the legs below the knees and hock a pressure which is nearly equivalent to the height of the vein; as a result the cells of the capillary wall are the seat of an increased exudation, and the legs accordingly 'fill,' a condition removable by exercise.

The **Movement of Lymph** is largely brought about by muscular contractions in the neighbourhood of the vessels, by which means they are compressed and their contents forced onwards, since the valves which the vessels contain prevent a back flow. The obstruction caused by the lymphatics passing through glands is not serious, while the involuntary muscle fibres in the capsule of the gland more than compensate by their contraction for any resistance in the gland itself. The pressure of the lymph in the lymph spaces is higher than that in the jugular vein, so the flow of lymph from the tissues to the vein is assisted by the fact that the fluid is passing from a region of higher to one of lower pressure. The movements of the diaphragm, tendons, and fasciæ produce an aspirating effect on the lymph circulating through them. In the case of the diaphragm the lymphatic vessels drain the two large lymphatic sacs the pleura and peritoneum. Owing to the direction taken by the fibres of the diaphragm, compression is exerted on the lymph spaces during its contraction, while a sucking action is produced when it relaxes. This pumping arrangement exists in tendons, fasciæ of muscles, etc., and is a valuable aid in lymph circulation.

Once the lymph from the abdominal viscera and hind quarters has found its way into the thoracic duct, its passage into the general circulation is favoured by gravity, by the muscular contraction of the coat of the duct and by the negative pressure produced in the anterior vena cava vein by the process of inspiration, while the aspiration of the thorax keeps the duct filled; the combined result of these forces is that the lymph is aspirated out of the duct into the vessel. This aspirating influence has been proved on the horse by experimental inquiry, a negative pressure in the thoracic duct having been observed during inspiration, and a positive pressure during expiration. In a manometer placed in the thoracic duct of the ox, Colin states that mixed chyle and lymph rose in five minutes to a height of over three feet; this pressure is one third of the blood pressure in the aorta, and appears excessive. The lateral pressure in a lymph vessel in the neck of the horse was from one half to three quarters of an inch of a weak solution of soda; in the dog the lateral pressure was half that found in the horse.

The thoracic duct terminates in the anterior vena cava at the jugular confluent in a variety of ways; its most usual method is that it dilates before entering the vein, and from the dilatation either one or two very short vessels are formed which enter the anterior cava, the entrance being guarded by a valvular arrangement. The right lymphatic channel also opens into the anterior cava at the jugular confluent, the entrance being furnished with a double semilunar valve. The blood in the vena cava vein is prevented from passing into the thoracic duct by the presence of these valves, which normally only allow fluid to pass in one direction, viz., from the duct into the vein. Colin has observed that it is not uncommon in the horse to find the lymph in the thoracic duct slightly blood-stained, a slight leakage from the vein into the duct being liable to occur in this animal, though such has never been seen in the ox.

The lymph moves slowly in its vessels. Weiss has observed a rate of from 9 to 11 inches (23 to 28 cm.) per minute in a large lymphatic in the neck of the horse, but the velocity in the small vessels is very much less.

Section 2.

Chyle.

In the thoracic duct the lymph from the body meets with the lymph coming from the intestines, termed chyle. This chyle is derived from the villi and passes up the mesentery by many vessels, which in the horse are said by Colin to number 1,200. Each of these passes through a lymphatic gland before entering the *receptaculum chyli*. Chyle is closely allied to lymph in its chemical composition, but it differs from it in containing during digestion a quantity of neutral fat, which gives it a milky appearance. The amount of this fat in dogs may vary from 2 per cent. to 15 per cent. or even more. The fat is partly in the condition of measurably large droplets, such as are seen in milk, but the bulk of it exists as extraordinarily minute particles; hence the name 'molecular basis,' which is applied to the fat particles in chyle collectively.

The Villi.—We have mentioned that in the ordinary tissues the radicles of the lymph-vessels are the lymph spaces, but in the wall of the small intestines the origins of the lymph-vessels are highly differentiated structures, known as villi and solitary glands. The villi (Fig. 59) are innumerable projections from the inner surface of the mucous membrane shaped like minute fingers; they are only found in the small intestines, and have been calculated by Colin to amount to forty or fifty millions in the horse and ox. In the interior and central part of the villus is a vessel termed the *lacteal;* it may be single or multiple, straight or branched, and at the base of the villus it opens by a valvular arrangement into the lymphatic system. Surrounding the lacteal is a network of capillary bloodvessels, while filling up the finger of the villus not otherwise occupied by vessels is a peculiar structure found especially in lymphatic glands and known as adenoid tissue (p. 245); this tissue is relatively larger in amount in the villi of carnivora than of herbivora (Fig. 60). Covering the entire villus is a basement membrane on which is set a layer of columnar cells, placed so that their narrowest end is next the basement membrane and their broadest next the interior of the intestine. The cells at their narrowest part are in touch with the adenoid tissue of the villus. Each cell contains a nucleus, and on that edge next the

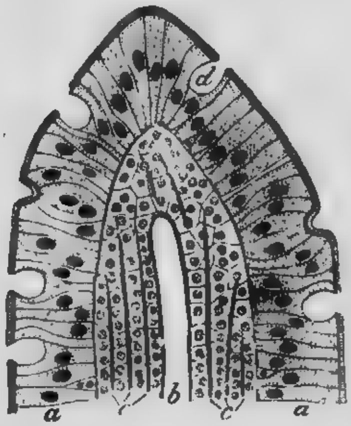
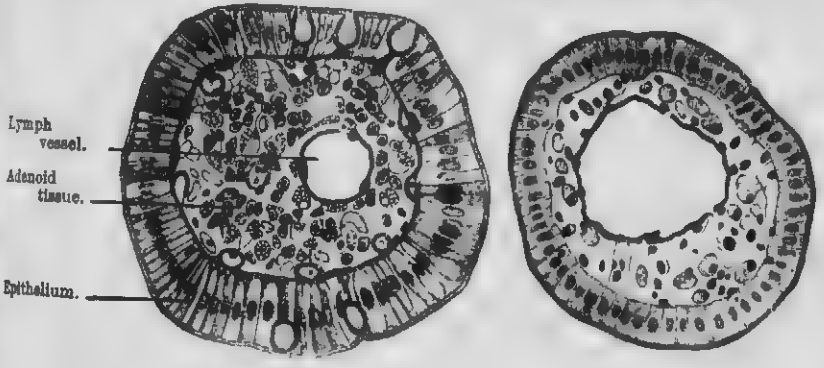


FIG. 59.—VERTICAL SECTION OF A VILLUS: CAT. × 300 (STEWART).

a, Layer of columnar epithelium covering the villus—the outer edge of the cells is striated; *b*, central lacteal of villus; *c*, unstriped muscular fibres; *d*, mucin-forming goblet-cells.

interior of the bowel is a clear band bearing fine striations. Lying between the columnar cells are others which from their shape are spoken of as 'goblet cells' (Fig. 59); by means of a pore they extrude their contents, consisting of a transparent material known as mucin, into the intestine. Within the villus are bands of involuntary muscle-fibre arranged parallel to the axis of the villus, by the contraction of which, combined with the peristaltic movements of the intestine, the capacity of the lacteal vessel is altered in such a way that it is alternately filled with lymph from the reticular adenoid tissue, and emptied of



DOG. RABBIT.

FIG. 60.—TRANSVERSE SECTION OF VILLI OF CARNIVOROUS AND HERBIVOROUS ANIMALS (WALLER, AFTER HEIDENHAIN).

The large cells in the epithelial zone of the dog are the goblet cells.

lymph into the lymphatic vessel at the base of the villus. This is known as the pumping action of the villus, and provides an important factor in the furtherance of the chyle (lymph) towards the thoracic duct.

The other lymph radicles found in the intestine are the *Solitary Follicles*, which are found studding the whole of the mucous membrane of the small intestines; these solitary follicles are at certain places in the ileum collected into masses where they are known as *Peyer's Patches*.

The **Solitary Follicle** is essentially a lymphatic structure and is not concerned like the villus in absorbing anything from the food. It consists of a mass of adenoid tissue, the network of which is filled with leucocytes; within the network are capillary bloodvessels, and surrounding the whole is a space across which branches of the adenoid network pass. This space is known as a *lymph space* or *sinus*; it is lined, like those previously described, with epithelioid plates, and opens into a lymphatic vessel. As the lymph passes through the adenoid tissue, some of the corpuscles found in the meshes of the network are added to it and become lymph corpuscles.

Chyle is a turbid fluid of alkaline reaction and a specific gravity of 1007 to 1022. In starving animals it is transparent owing to the absence of fat, and it is, in fact, at this time practically pure lymph. Colin observed that the chyle of herbivora was yellowish or yellowish green; it is possible that this colour may be due to chlorophyll taken up from the food. In the horse, as collected from the thoracic duct, it is often reddish, due, no doubt, to a slight leakage from the vena cava, such as has been previously noted (p. 253).

In the small intestines of the horse, it has been observed by Colin that almost immediately after food has been given, waves of chyme are passed into the duodenum from the stomach; in consequence the lacteals in the mesentery in connection with this portion of intestine become opaque, though previously they were filled with a colourless fluid. As the chyme passes along the bowel the other lacteals in their turn become opaque, until at last the whole of them are filled with this milky fluid. Colin draws especial attention to this regular invasion of the lacteals from the duodenum to the ileum.

The movement of chyle is due to the muscular contraction of the intestinal villi forcing it onwards, while the valves in the lacteals prevent its return.

SECTION 3.

Absorption in General.

The activity of absorption, especially in the horse, has been made known to us by the experiments of Colin.

Absorption from the Respiratory Passages is remarkably rapid. Colin showed that potassium ferrocyanide could be detected in the blood two minutes after being injected into the trachea, and that it appeared in the blood before it was found in the chyle; the same salt was also found in the urine eight minutes after being introduced into the trachea. A solution of nux vomica injected into the trachea produced tetanic symptoms in three minutes; turpentine, alcohol, and ether were also rapidly absorbed, but oil could not be taken up, and was rejected by the nostrils.

Such drugs as morphia, pilocarpin, physostigmin, etc., are all rapidly absorbed from the air-passages,[*] and according to our observations produce their physiological effect in a shorter time than when simply injected under the skin. The lungs also have the power of absorbing certain poisons like curare, which are not absorbed when introduced into the digestive canal. The absorption of water from the bronchial passages is very rapid. Colin introduced six quarts of water per hour into the trachea of a horse; the animal was destroyed at the end of 3½ hours and no fluid was found in the bronchi. He also poured into the air-passages one pint of water at a time; repeating this without intermission, he poured in 74 pints of water before he caused death. So rapid is absorption from the bronchi, that a horse may be placed under chloroform almost instantaneously by an intra-tracheal injection of the drug.[†] The rapidity of absorption is therefore very great, but in spite of the facility with which drugs are taken up, the lining membrane of the bronchial tubes is remarkably tolerant of such irritating agents as turpentine, strong liquid ammonia, acetic acid, etc., and offers in a state of health an almost impassable barrier to putrid organic infusions, or at any rate these do not appear to produce any local irritation when injected.

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[*] It is interesting to observe that the injection of liquids into the trachea (either high up, or as low as its bifurcation) excites the reflex act of swallowing, probably due to stimulation of the recurrent nerve.

[†] It is not intended here to recommend the intra-tracheal administration of chloroform, which is not only dangerous but produces the greatest excitement in the patient.

Absorption from the Cellular Tissue is very active, and both the bloodvessels and lymphatics take part in the process; ferrocyanide of potassium injected into the face has been detected in a carotid lymphatic in seven minutes. The rapidity of cellular tissue absorption is hastened by muscular movement.

Absorption from the Conjunctiva is very pronounced for some drugs such as atropin and certain organic poisons, but there are others which are not absorbed so readily. Curare is not absorbed through the conjunctiva, and Colin could not infect horses with anthrax by placing anthrax blood and fluids in the conjunctival sac.

Absorption by the Skin, if the surface be unbroken, is slow even for those drugs which will pass through it, while there are many organic and inorganic substances which refuse to pass through the unbroken epidermis. Colin kept the lumbar region of a horse wet for 5 hours with a solution of ferrocyanide of potassium; the salt was detected in the urine in 4½ hours, although the skin was quite unbroken. From a wound or abraded surface, absorption will occur rapidly with some agents, slowly with others. Colin placed a horse's foot with a wound on the coronet in a solution of ferrocyanide of potassium; in 20 minutes he detected the salt in a lymphatic of the thigh. In connection with absorption from a wounded surface, he found that the poison was taken up quite as readily by the lymphatics as by the bloodvessels.

The mucous membrane of the vagina is found by experiment to absorb very slowly.

Experiments made on **Absorption from the Pleural and Peritoneal Cavities** showed that such drugs as strychnin rapidly produce fatal symptoms when injected into these sacs; even in such a short time as from 3 to 7 minutes tetanic symptoms supervene. Potassium iodide injected into the peritoneal cavity of a sheep may be detected in the thoracic duct 5 to 8 minutes after the operation.

Starling and Tubby have shown, however, that the active agents in absorption from these sacs are the blood-vessels, and that the share taken by the lymphatics is insignificant. If methylene blue be injected into the pleural cavity the dye appears in the urine long before any trace of colour can be perceived in the lymph flowing from the thoracic duct.

Stomach absorption, or rather its absence in herbivora, has been dealt with at p. 176. Even in the dog it is now admitted that absorption is by no means so certain as was at one time supposed. Water for instance passes through the stomach and undergoes no absorption; salts are only absorbed with difficulty; sugars and peptones are taken up, but only if in sufficient concentration; ordinarily they are absorbed with difficulty.

Intestinal Absorption.—The absence of stomach absorption in the horse and ox points to intestinal absorption as being of considerable importance in herbivora. That this absorption is very rapid is proved by Colin's experiments. Hydrocyanic acid injected into the small intestine of a horse caused death in 1 to 1½ minutes, and potassium ferrocyanide injected into the bowel, after tying the mesenteric lymphatics, was detected in the blood 6 minutes afterwards.

The Paths of Absorption.—The paths by which intestinal absorption occurs are (1) through the villi into the lacteals, and (2) through the bloodvessels into the venous system. This points to the possibility that some substances taken up from the bowel may at once pass into the blood viâ the thoracic duct (Fig. 61), while others must first proceed to the liver by the portal vessels for further elaboration before entering the blood.

It will be remembered that the villi are found only in the small intestines; in the large intestines there are no villi. It must not, however, be supposed that absorption in the latter is exclusively carried on by the bloodvessels, for remembering the large chain of glands, along the colon in particular, it is probable that the material absorbed passes through these glands to a greater or less extent, as in the mesentery, before entering the circulation. There is, at any rate, a well-developed lymphatic system in the walls of the large intestine, and it is certain that material is taken up from this bowel both by the bloodvessels and lymphatics. The amount of this must be considerable, when the size of these bowels is borne in mind and the character of their contents.

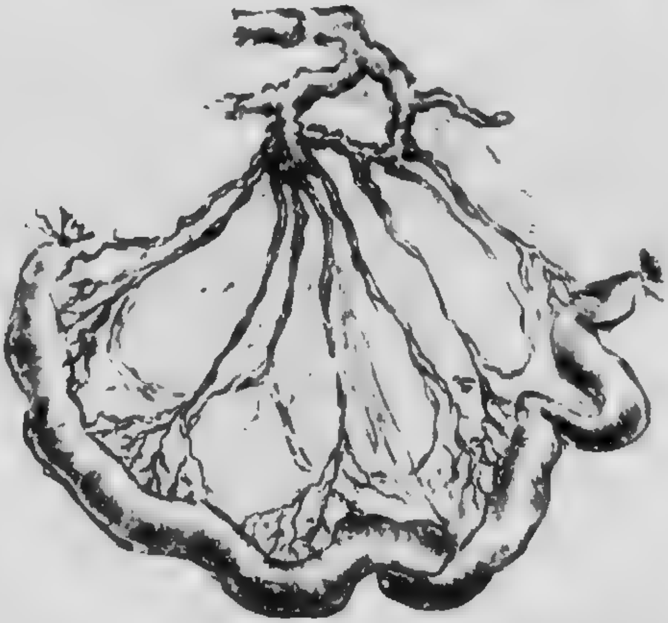
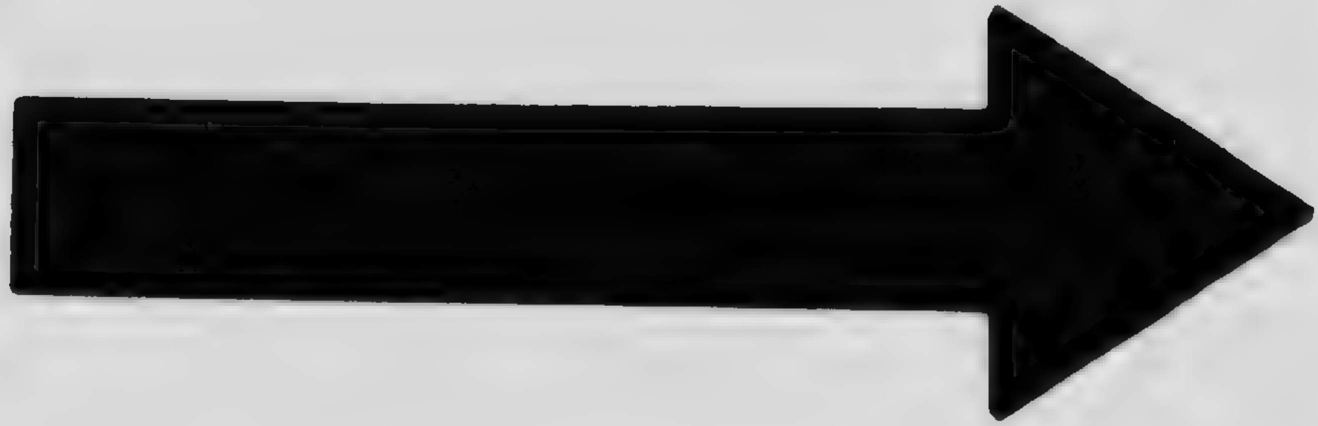


FIG. 61.—LOOP OF SMALL INTESTINE OF THE HORSE DURING ACTIVE ABSORPTION, WITH DISTENDED LACTEALS.

Substances can be taken up with extreme rapidity from the large bowels. Colin observed that 18 minutes after injecting a solution of nux vomica into the cæcum of the horse convulsions began, and 8 minutes later the animal was dead. Anæsthetics, such as ether, may also be administered per rectum and produce narcosis. Finally, and from some points of view most important of all, proteids may be absorbed from the rectum and single colon, in spite of the fact that there is no proteolytic ferment to render them soluble.

Absorption of Fat.—If a cannula be placed in the thoracic duct of a starving dog, the lymph which escapes is identical with that from any other part of the body. If the animal be now fed on a diet rich in fat, the lymph becomes milky, and even the blood plasma becomes turbid from fat, if the contents of the duct are permitted to enter the general circulation. It is evident that the lymphatics are the path by which the fat enters the body, for comparative analysis of the blood of the portal vein and carotid artery shows that the amount of fat in the two is the same. The blood-vessels, therefore, have nothing to do with the absorption of fat, yet from an open thoracic duct not more than 60 per cent. of the total fat given in an experimental diet can be recovered; after deducting that excreted unabsorbed with the fæces, there still remains a balance unaccounted for. The fate of this missing portion of fat is still a matter of conjecture.

It has been shown (p. 236) that fat in the small intestine is both saponified and emulsified, the former being a chemical, the latter a physical change. These processes result from the separate and combined action of the pancreatic juice and bile, and they lead to two possible views as to the mechanism of fat absorption. Emulsification reduces the fat (and fatty-acids) to a state of subdivision into particles so minute that they might conceivably be simply passed as such, through the epithelial cells of the villi to the lacteals, by an activity of these cells comparable to the ingestive powers of a white blood-corpuscle. This would readily account for the appearance characteristic of chyle (p. 253), the minuteness of the fat particles it contains being probably intended to prevent embolism by plugging of the capillaries. The view thus indicated was the one



MICROCOPY RESOLUTION TEST CHART

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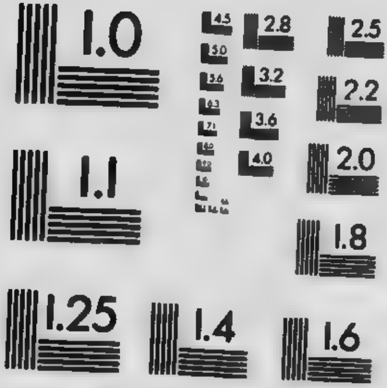

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formerly most prevalent. On the other hand, bile has, in virtue of its bile-salts, an extremely active solvent action on both fatty acids and soaps: hence the possibility that fat is split up so as to give rise to variable relative amounts of fatty-acid and soap, which then pass *in solution* into the cells of the villi, as do the proteids and carbohydrates.

If the intestinal mucous membrane of an animal in full fat absorption is stained with osmic acid the epithelial cells are found to be crowded with minute particles of varying size, whose blackness shows them to be fat (Fig. 62). This fact provided the chief support for the view that fat reaches the lacteals in a state of minute mechanical subdivision not necessarily involving much chemical change. If this were so we should expect to see some of the fat-particles in transit through the striated border of the epithelial cells, and this is never observed. But if we hence discard the first possibility and accept the more current view that fats are absorbed in solution, we must assume that there is a rapid reconstruction of neutral fats inside the epithelial cells after the absorption of the dissolved soaps or fatty-acids, inasmuch as the cells still *always give* with osmic acid the appearance characteristic of the presence within them of minute fat-particles. This synthetic reconstruction of fat may possibly be brought about by the reversible activity of the lipase ferment to which we referred on p. 237,

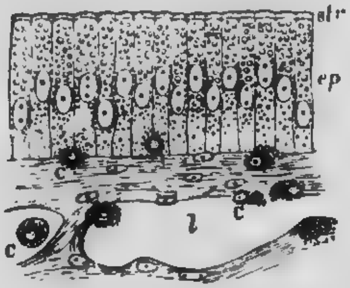

FIG. 62.—MUCOUS MEMBRANE OF FROG'S INTESTINE DURING ABSORPTION OF FAT (SCHÄFER).

ep, Epithelial cells; *str*, striated border; *c*, lymph corpuscles; *l*, lacteal.

though it is more probably due to the constructive activity of the cell-protoplasm. This second view of the mechanism of fat-absorption further enables us to understand the all-important rôle of bile in the absorption of fat.

Absorption of Carbohydrates. — The digestive changes undergone by starch are described on p. 142. The sugar formed from starch by the saliva is maltose, the maltose by the aid of the succus entericus and epithelial cells of the intestine is converted into glucose, this and its allies being the only form in which sugar can be utilized by the system; both cane and milk sugar must be thus converted or else they are excreted in the urine. It is clear from what has been said that the path of absorption for carbohydrates is the bloodvessels.

Absorption of Proteid.—If the thoracic duct of a dog be ligatured and a large proteid meal given it is perfectly absorbed, as shown by the increase in urea, while there is no increase in the amount of lymph or of its proteid contents. This clearly shows that the absorbed products pass into the bloodvessels. Proteids before absorption are rendered soluble by conversion into peptones and proteoses, yet there is no blood in the body, including that of the portal area, which is found to contain even a trace of peptone or proteose; in fact, the presence of these substances in the blood acts as a poison, giving rise to peptonuria. The peptones and proteoses enter the blood as ordinary proteid, so that during their passage through the epithelial wall of the intestines they become regenerated. Beyond the above facts, very little is known of the absorption of proteid.

Absorption of Water and Salts.—These are taken up by the bloodvessels and with remarkable rapidity. The amount of water capable of absorption is very considerable. The material passes into the bloodvessels either through the epithelium or between the epithelial cells.

CHAPTER VIII

DUCTLESS GLANDS AND INTERNAL SECRETIONS

THE **ductless glands** of the body are represented by the spleen, thyroid, thymus, adrenals, pituitary, and pineal bodies. The function of these is either imperfectly known or entirely unknown, but within recent years experimental enquiry has thrown some light on their use as glands producing an *internal secretion*, viz., a something carried away by the blood or lymph stream and utilized elsewhere by the body.

Internal secretions are not limited to ductless glands. It is now known that the pancreas, liver, and other glands produce, in addition to the visible secretion passing away by their duct, another or internal secretion passing away by lymph or blood channels, and quite distinct from the ordinary fluid secreted by the gland (see also p. 285).

The discovery of *secretin* (p. 233) by Starling and Bayliss opened up a field of the highest importance, possessing possibilities the extent of which cannot be forecast. In secretion we have a specific chemical excitant, or *hormone*, and it may yet be shown that secretions which have been regarded as due to the influence of the nervous system are in reality produced by a chemical stimulant furnished by the body itself. Edkins, indeed, considers this is so of the gastric juice; while Starling and Bayliss point to the specific chemical excitant theory as offering some explanation of the sympathy between the uterus and the mammary gland, the occurrence of menstruation, and periodic sexual excitement in the lower animals. The ovary has been suggested as the seat of production of such chemical excitant. The corpus luteum is regarded as a ductless gland, its internal secretion being connected with the fertilization and implantation of the ovum. The influence of the ovaries on the development of the external genital organs may also in this way be explained, for the arrested development which occurs as the result of removing the ovaries in the young animal is prevented by implanting them in a distant part of the body. The sympathy between ovaries and mammary glands is further shown by the remarkable fact that a cow ovariotomised when in *full milk* remains in milk for two or three years. The influence of the ovaries on psychic conditions is well recognized: some forms of vice in the mare are cured or improved by removal of the ovaries. It is to be noted that apparently the complete removal of all trace of ovarian tissue in the cat and dog may not invariably prevent periodic sexual excitement (Leeney). It has been stated that the removal of the ovaries from the dog affects metabolism, especially the consumption of oxygen, which falls off, and that this may be neutralized by the administration of an extract of ovary; this causes the metabolism to rise above the normal, but does not affect the un-operated animal.

Similarly, there can be no doubt as to the testicles forming an internal secretion. It is fair to assume that among other functions the implantation of the characteristics of the male, especially the aggressive characteristics, must be regarded as part of its duty. Otherwise it is difficult to account for the alteration in character which occurs as the result of complete castration, and the modifying change which follows from leaving some of the epididymis attached to the cord. The influence of the testicles on the growth of bone is recognized in man; the long bones continue to grow, due to the delay in the ossification of the epiphyses; the same is said to have been observed in animals. The effect of castration on the eating properties of flesh is well known. The influence on the thymus gland is very marked; instead of disappearing at puberty, castration causes the gland to become larger and more persistent. The effect of removal of the testicles and ovaries, on the dog, cat, deer and birds, may be conveniently considered in the chapter on 'Generation and Development."

The adaptation of the digestive fluids to the nature of the food has been referred to (p. 170). This and the influence of a fixed diet in producing a more effective digestive secretion, and the harm resulting from sudden changes in diet (p. 287), may possibly be regulated by a specific chemical excitant. These are matters of the highest practical importance in the feeding and management of animals.

The chief lesson that the present work on internal secretions teaches is that an organ apparently functionless may be performing some office of the highest importance, while even those actively employed in the preparation of an obvious secretion may, in addition, be carrying out important chemical activities—the liver, for example, with its external secretion of bile and its internal secretion of urea and glycogen; the pancreas, with its digestive fluid, and its invaluable internal secretion, which regulates the destruction of sugar. Even the kidney, in all probability, possesses an internal secretion affecting metabolism. The spleen, on the other hand, would appear to possess neither an internal nor an external secretion, for it has frequently been removed without ill effects; but the question must be dealt with in a little more detail.

The **Spleen**, in spite of the numerous observations to which it has been subjected, is still a physiological enigma. Its vascular arrangement is peculiar in that it is capable of holding a considerable quantity of blood, and for this purpose readily lends itself to change of size. Further, it is the only tissue in the body where the cell elements are directly bathed in blood without the intervention of even a capillary wall. The spleen contains a considerable amount of involuntary muscular fibre and is capable of movement. These movements have been carefully studied, and it is established that they are of two kinds, a slow expansion which occurs after a meal followed by contraction, and a rhythmical expansion and contraction occurring in certain animals, such as dogs and cats, at intervals of about one minute. It is believed that the latter movement is for the purpose of assisting the circulation through the organ, to which the splenic pulp offers considerable resistance. That the movement is brought about by the bands of involuntary muscular fibre is undoubted; the spleen is liberally supplied with motor nerves, and stimulation of these leads to a reduction in the volume of the organ. It is even believed that there may be nerves to the spleen, which produce dilatation.

The *use of the gland* is largely based on conjecture. By some it has been considered the seat of formation of red blood-corpuscles, and that this function is present during intra-uterine life and shortly after birth is undoubted; but there is no evidence of this function in the adult. It has been claimed to be the seat of destruction of the red cells and of phagocytosis, and on this point there are some telling facts; for instance, certain large amœboid cells found in the spleen are capable of ingesting and destroying worn-out blood-cells and other solid matter such as micro-organisms, while the richness of the splenic pulp in iron is regarded as due to the hæmoglobin of the destroyed red blood-cells. The theory is very plausible though by no means definitely proved; at the same time there is great difficulty in getting away from the fact that the spleen appears in every way to be admirably suited to act the part of a blood filter.

The lymphoid tissue of the spleen, like that of lymphoid tissues in general, is capable of forming a substance from which uric acid may be readily produced, and the spleen has in consequence been regarded by many as the seat of active metabolic changes with the formation of uric acid. The evidence, however, is not sufficiently conclusive to warrant our regarding uric acid as a special product of the spleen.

Some physiologists have suggested that the spleen produces an enzyme which converts trypsinogen into trypsin. There is no reason why the spleen might not do so, but it by no means follows that this is normally its function, nor would there appear to be any necessity for this action in face of the fact that it is one of the special functions of the intestinal juice.

In connection with all these theories it is well to remember that the spleen may be removed completely and no ill effects follow.

Thyroid.—Some of the most interesting work on the ductless glands has been carried out on the thyroid, and it is largely to this body that such little knowledge as we as yet possess of internal secretion is mainly due.

For years it had been observed that atrophy or absence of this gland in the human subject was associated with arrested development both mental and physical; the man so affected remained a child both in intelligence and appearance. This stimulated experimental enquiry, and the thyroids were removed in many animals, the majority of carnivora dying as the result, while half of the herbivora recovered from the operation. So contradictory were the results obtained by different observers on the gland and its uses, that the whole question was submitted to very close enquiry, which revealed the fact that the ordinary thyroid consists of two distinct portions, one part the *thyroid* proper, the other the *parathyroid*. In most animals much the same results are obtained when both parts are removed, but when the parathyroids alone are excised, death rapidly ensues, preceded by convulsions. The removal of the thyroid only gives rise to a train of symptoms accompanied by chronic wasting, much slower in development than in the case of the parathyroids. Such are the broad lines of distinction between the two portions of the combined thyroid body. The colloid substance constitutes the internal secretion of the thyroid, but forms no part of the secretion of the parathyroids; and histologically while the former consists of vesicles lined by a single layer of cubical epithelium, the parathyroid is composed of columns of epithelium-like cells. The gland contains a nucleoproteid and colloid substance; the latter is not a nucleoproteid, and is remarkable for containing iodine in organic combination with the proteid. The iodine-containing substance is termed *iodothyrin*; it is a brown amorphous material, containing phosphorus and 10 per cent. of iodine.

As to the uses of these bodies little is known. That they produce an internal secretion which finds its way into the system by the bloodvessels or lymphatics is certain; it is probable that this secretion is mainly directed to the nutrition of the body, especially of the central nervous system. Some have considered that the gland produces a substance which neutralizes poisons formed during metabolism. The consensus of evidence is that an internal secretion is produced which is essential to the body. It appears beyond all doubt that when from any cause the gland fails to supply the secretion, the symptoms may be relieved by the administration of an extract of the thyroid body, or even by feeding the patient on the prepared gland.

Thymus.—This body, composed of modified lymphoid tissue, is mainly of use in fœtal and very early life; later on it atrophies. Nothing is known of its function, though it is observed that castration appears to have an effect on its disappearance, as the process of atrophy is much slower in the castrated as compared with the uncastrated animal, while its early removal has been observed to be associated with a rapid growth of the testicles.

The experimental removal of the **Adrenals** in any animal is rapidly followed by death, preceded by symptoms of great muscular prostration and diminution of vascular tone. In Addison's disease in man these bodies are affected, and give rise to much the same symptoms as above, and in addition bronzing of the skin is present. Like the thyroids the adrenals consist of two distinct tissues, a medulla which can be shown to be derived during the process of development from the sympathetic nervous system, while the cortex is formed from the mesoblast. While nothing is known of the function of the cortex, the medulla yields under experimental enquiry some remarkable and characteristic results.

An extract of the medulla of the gland when injected into the blood causes a marked increase in blood pressure; even extremely small doses produce this effect. If the vagi are intact the heart-beat is simultaneously slowed, if cut the beat is quickened. The active agent is known as *adrenalin*, and its effect on the circulation in causing constriction of the small vessels is so marked as to be turned to account in minor surgery. The result of the constriction of the vessels is a rise in blood pressure, and this is not necessarily central in origin, as it may be obtained after the constrictor centre in the spinal cord has been destroyed. Adrenalin acts upon all plain muscle and gland cells which receive sympathetic fibres, and it is distinctly noteworthy that the effects, whether they be augmentory or inhibitory, are identical with those produced by stimulation of the sympathetic fibres (Langley), of which system the medulla of the gland is, as pointed out above, merely an outgrowth.

It is probable that the function of this gland is concerned in the provision of a substance intimately connected with muscular metabolism, especially 'tone,' not only of the skeletal muscles, but also of the muscular fibres of the circulatory system. There is also considered to be some connection between the adrenals and the sexual system. In rabbits the cortex of the gland becomes twice the normal thickness during pregnancy; and it is believed that in man a connection exists between the adrenals and the growth of the body, the development of puberty, and sexual maturity.

Very little is known of the function of the **Pituitary Body**. The part has been experimentally removed, and in such cases muscular weakness, twitchings, and a lowered temperature have been observed. The pituitary is closely allied to the adrenals in the effects on the circulation of extracts made from it, while in its general metabolic functions it is considered to be related to the thyroid. In man the singular disease *acromegaly*, characterized by an overgrowth of the bones of the face and extremities, is associated with disease of the pituitary body.

Nothing is known of the uses of the **Pineal Body**. It is regarded as the dorsal eye of a remote ancestor.

CHAPTER IX

THE SKIN

It is obvious that one important function the skin performs is that of affording cover to the delicate parts beneath; wherever the chance of injury is the greatest the skin is the thickest, while in those parts where sensibility is most required it is thinnest. The skin of the back, quarters, and limbs are good examples of the first type; on the back especially a protective covering is found which, in some horses, is as much as a quarter of an inch in thickness: the face and muzzle are a good example of the latter variety, the skin in some parts being as thin as paper. In those regions not exposed to violence it is also thin, as on the inside of the arms and thighs. In spite of the thinness of the skin its strength is remarkable; a horse's body may be dragged along by the thin skin of the head.

The skin as an organ of touch is of great importance. All animals appear most sensitive to even slight skin irritation; flies will cause horses considerable suffering, and the elephant, with its thick hide, is quite as intolerant of these tormentors as is a well-bred horse. The skin is highly endowed with sensory nerves, especially that part connected with the organs of prehension; the long hairs, 'feelers,' growing from the muzzle of the horse end in special tactile structures in the skin (Fig. 63).

The skin is a bad conductor of heat, and this is considerably assisted by the layers of fat found beneath or at no great distance from it, as in the abdominal region; it is the subperitoneal fat which protects the viscera of animals living in the open and lying in wet places. The epidermal covering of the skin relieves the parts beneath from excessive sensitiveness; through the sebaceous secretion it assists in preventing loss of heat, while the greasy covering helps the hair to throw off rain, prevents the penetration of water, and so saves the epidermis from disintegration. Horn is skin which has undergone a modification.

Hair.—Not all parts of the body are covered by hair. There is very little on the muzzle and lips, and it is very scanty on the inside of the thighs, inside the cartilage of the ears, and on the mammary gland and genitals. By means of the hair the heat of the body is maintained and prevented from passing off too rapidly. The thickness of the hairy covering varies considerably with the class of horse: the better bred the animal the finer the coat. Draught horses yield between 7 lbs. and 8 lbs. of mixed hair, dirt, and dandruff by clipping; in a well-bred horse this would be reduced to 10 oz., or even less; the amount of hair of the mane and tail is about 1½ lbs. It is a well-known fact that, excepting the hair of the mane and tail, that of every other part of the body has only a temporary

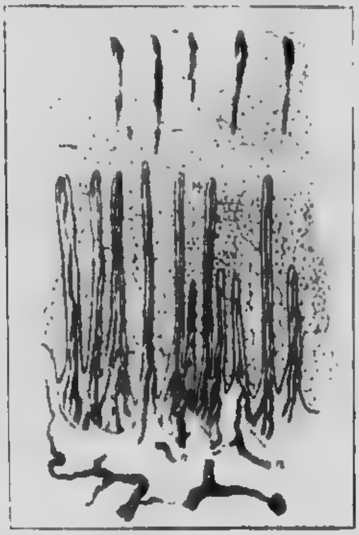

FIG. 68.—SECTION OF MUCOUS MEMBRANE OF THE HORSE'S LIP, SHOWING THE NERVE ENDINGS IN THE TOUCH PAPILLÆ.

existence, and is changed twice a year, once for a thick, and once for a fine coat. During this period horses are generally regarded as not being at their best, and changing the coat is always urged as a cause of loss of condition or stamina. The permanent hair is not entirely represented by that of the mane and tail, the eyelashes are permanent, also the long tactile hairs on the muzzle. The temporary hairs on the horse are of two kinds which can only be distinguished by their rate of growth. If a part be clipped, or, preferably, shaved and the growth watched, in a short time it will receive a scanty covering of long rapidly growing hair, followed by a slow growth of ordinary hair. There is no difference in the two hairs excepting the length. The long rapidly growing hairs are known as 'cat hairs'; they are not numerous, being about 27 to the square inch, while the ordinary hairs are about 4,800 to the square inch.* The growth of the hair is regulated by the surrounding

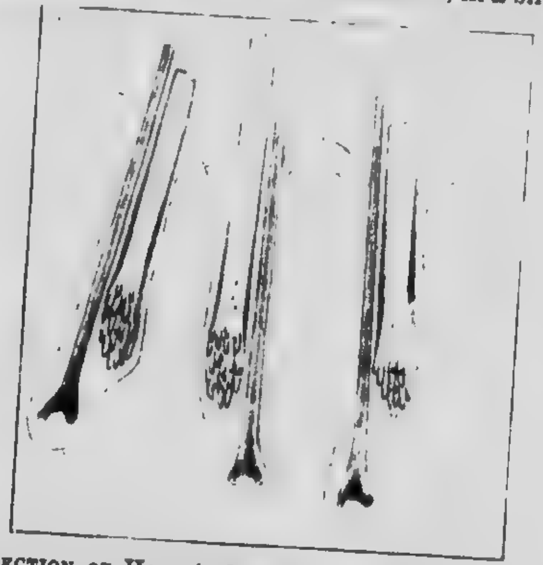

FIG. 64.—SECTION OF HORSE'S SKIN, SHOWING THE CASTING OFF OF THE OLD HAIR AND GROWTH OF THE NEW.

It will be observed that both are emerging from the same follicle.

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* I am indebted to Major Newsom, Army Veterinary Corps, for the trouble he has taken in making this tedious calculation.

temperature; if horses in the depth of winter are placed in a heated atmosphere, such as a horse deck on board ship, the majority commence to shed their winter coat in a few days, though the temperature of the outside air may be at freezing-point; similarly, if taken from a warm to a cold locality the hair responds by becoming longer. Speaking generally the above statements are correct, but there are exceptions and modifications. Some horses do not shed their coat after passing into a warmer latitude; the mechanism which regulates the periodical shedding of hair refuses to respond to the changed condition of affairs, so that in passing from north to south of the Equator with its reversal of seasons, the animal may grow a summer coat in winter and *vice versa* for at least a year after entering the new latitude. The permanent hair of the body, viz. the mane and tail, may grow to almost any length, but the temporary hair of the surface of the body only grows to a definite length. The full length having been attained nothing will make it grow longer, yet if the horse be clipped hair at once grows rapidly, but only to its original length; in other words, everything is present for the needful growth to occur, but there is a restraining influence present which determines the length of hair according to the season.

Of the **pigment in hair** which gives colour to the coat our knowledge, until quite recently, has been of the scantiest kind. The active investigation now being carried out of Mendel's theories of heredity, when applied to the special case of heredity in coat-colour, made it essential to know more about the origin, nature, and behaviour of the hair pigments, and so we now have some information which is both interesting and promising.*

Using the name in its generic sense, three different forms of 'melanin' are found in hairs—black, chocolate, and yellow. Of these the black is extremely insoluble, and hence very difficult to deal with; as also is the chocolate pigment, though to a less extent. The yellow, on the other hand, dissolves readily in numerous solvents, and may thus be easily obtained. In its reactions it differs entirely from the black and chocolate pigments. In the case of mice there is now no doubt that their varying colours are due to the presence in their hairs of one or more of these three pigments. The less numerous experiments so far made with horse-hairs, which are, however, to be carried out shortly on a large scale, suggest no doubt as to the different colours of horses being due to causes essentially the same as those which give the various colours to mice. As to the origin of these pigments, it has generally been presumed that they must be derivatives of hæmoglobin, but there are no pathological or purely chemical facts in definite support of this view. On the other hand, it has been shown* that an extract can be made from the skins of rats, rabbits, and guinea-pigs, which acts on tyrosine (see p. 236) in such a way as to give rise to pigment substances. From the conditions under which the conversion is most readily effected, and the fact that the activity of the extract is at once destroyed by boiling, the active agent is regarded as a ferment, and, in accordance with the systematic nomenclature now used, is therefore known as *tyrosinase*. A further fact of extreme interest is that the colour of the pigment formed from tyrosine corresponds to the colour of the animal from whose skin the active extract is made. Black pigments are produced when animals are used whose skin contains black pigment, and yellow substances are obtained when the skin contains orange pigment. With the exception of black and grey horses which are liable to turn grey or white, all other colours are practically permanent even to old age. We do know, however, that injuries to the skin of horses, even of a slight character, are commonly followed by a growth of perfectly white hair, which never regains its pigment.

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* Florence M. Durham (Proc. Roy. Soc., vol. lxxiv., p. 310, 1904), and further researches as yet unpublished.

Experience shows that the heavy winter coat grown by horses is the cause of considerable sweating at work, and the general practice of clipping has hence been introduced.

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* *Loc. cit.*

Of its value there can be no doubt; it considerably reduces the risk of cold and chest diseases, for animals on coming in from work may be readily dried and thus protected from chills. Horses which sweat freely at work soon lose 'condition'; our observations have shown that this is due to the proteid lost by the skin, for, as we shall presently see, proteids are regularly found in the sweat of the horse. Clipping largely prevents this loss. The influence of clipping on temperature is dealt with in the chapter devoted to 'Animal Heat.'

In some animals, as for instance the dog and cat, the hairs are rendered erect under excitement such as anger or fear; this is due to the involuntary muscle attached to the hair follicle, and the process is under the influence of the sympathetic nervous system. The fibres for the body hair emerge from the spinal cord by the inferior roots, pass to the grey ramus of the sympathetic chain, and run to the skin by the dorsal cutaneous nerves; the fibres for the head and neck are in the cervical sympathetic. Under the influence of cold the hairs on the horse's body may become erect, but there is no indication of this under physical excitement, as in the case of the dog and cat.

It is possible that the prescience of a coming storm or change of weather exhibited by cattle may probably be due to the highly hygroscopic properties of their hair. Hair is one of the few organic substances which elongate instead of shorten as they grow moist. The effect of movement of every hair on the surface of the body may cause a mechanical stimulation of the hair-follicle nerves, and so gives rise to an uneasiness which presages the coming change.

Sweat.—By means of glands in the skin a fluid termed 'sweat,' and a fatty material known as 'sebum,' are secreted. Sweat, or perspiration, is not found to occur over the general surface of the body in any other hairy animal than the horse. There are certain parts of the skin which sweat more readily than others; the base of the ears in the horse is the first place where sweating begins, the neck, side of chest, and back follow, lastly the hind-quarters. No sweating takes place on the legs; the fluid found there has run down from the general surface of the body. Mules and donkeys sweat with difficulty, and then principally at the base of the ears. The ox sweats freely on the muzzle, and sweating even from the general surface of the body has occasionally been observed. It has been said that sheep perspire, while it is certain that both the dog and cat, especially the latter, sweat freely on the foot-pads as also on the muzzle, though not on the general surface of the body. The sweating of the pig is confined to the snout.

The secretion of sweat is continuous. When excreted in small amounts it evaporates as fast as it is formed, passing off as the insensible vapour which is always rising from the surface of the skin, and is known as 'insensible perspiration.' When the secretion is rapid and copious or the surrounding atmospheric conditions are unfavourable to its evaporation, it collects on the skin as that visible fluid material which is ordinarily termed 'sweat.' Colin gives various numerical statements respecting the insensible perspiration, from which we gather that 14 lbs. of water probably represent this loss in the horse for 24 hours. Much depends upon the humidity and temperature of the atmosphere; the drier and hotter it is, within certain limits, the greater the insensible perspiration.

The **amount of sweat** secreted daily can only be roughly determined; there are many conditions which affect it, such as the length of coat, nature of the work, and pace. Grandeau by estimating the total water consumed in the food and drink, and that voided in the urine and fæces, arrived at the amount of vapour passing away in the breath and perspiration. The mean amount of water evaporated daily by these two channels under different conditions of work was as follows:

At rest - - - -	6·4 lbs.
Walking exercise - - -	8·6 ,,
At work walking - - -	12·7 ,,
Trotting - - - -	18·4 ,,
At work trotting - - -	20·6 ,,

In each case the distance walked and trotted and the load drawn were the same. It is unfortunate that we have no means in the above experiments of determining the proportion which the water of respiration bears to that of perspiration.

Evaporation from the surface of the skin is a most important source of loss of heat; so marked is this in the horse that the resulting fall in temperature may even carry it below the normal, if the sweating be very profuse or the wetted area a large one.

The compensating action existing between the kidneys and skin observed in men exists also in the horse, viz., when the skin is acting freely less water passes by the kidneys, and *vice versa.*

Sweat obtained from the horse is always strongly alkaline; after filtration it is the colour of sherry, which is probably accidental, and due to contamination with dandruff, which contains a pigment, chlorophyll; it possesses a peculiar horse-like odour, and has a specific gravity of 1020. We found horse's sweat to have the following composition:*

		Containing.	
Water	94·38		
Organic matters	0·52	Serum albumin	0·105
		„ globulin	0·327
		Fat	0·002
Ash	5·10	Consisting principally of potash, and soda, chlorides, some magnesia, a little lime, and traces of phosphates.	

The proteids are thus seen to be serum-albumin and globulin, and their constant presence has been determined by a number of observations; the mineral matter is very high and consists principally of soda and potash, especially the latter. It will be observed that the mineral matter greatly exceeds the organic matter; in horses which have sweated freely the matted hair (which is due to albumin) is often seen covered with saline material, looking like fine sand. There appears to be some complemental action between the skin and the kidneys in the elimination of soda and potash; during rest the kidneys eliminate these salts, whilst during work they are assisted by the skin. Urea is also probably present in sweat (see p. 283). It is difficult to see why horses should excrete albumin by the skin; the loss thus produced accounts for the great reduction of vitality and strength in animals which sweat freely at work, and for which clipping is the only preventive.

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* 'The Sweat of the Horse,' *Journal of Physiology*, vol. xi., 1890.

Nervous Mechanism of Sweating. — A skin may sweat under quite opposite conditions, viz., both with a hot flushed skin and a bloodless cold skin, in others words an animal may sweat when it is hot or when it is cold. The former is a physiological condition and regulates, as we shall see, the body temperature; the latter is abnormal, but it occurs and disproves at once any notion of sweating necessarily depending upon a congested condition of the vessels of the skin. Experiments show that most of the features of sweating can be accounted for through the agency of the nervous system. Though we are ignorant of the manner in which the nerves terminate in the sweat glands, still it is certain that there are special branches of nerves, whose function it is to determine the secretion of sweat, and these are quite distinct from those which regulate the vascular supply. If the peripheral end of the divided sciatic in the cat be stimulated the foot-pads sweat; the proof that this reaction is a specifically nervous one is easy, apart from the fact that stimulation of the sciatic causes a violent constriction of the bloodvessels in the leg, for the sweating occurs when the leg has been cut off or the aorta tied, and it is absent under the influence of atropin. The effect of atropin on the sweat glands is very closely allied to its action on the salivary glands (p. 146); it paralyzes the secretory nerves which produce sweat.

As with the salivary glands, so in the present case secretion is not due to any increased supply of blood. It is true that in normal sweating, as is so readily seen in man, the skin is flushed as the increased secretion takes place, but the increased blood supply which the flushing indicates is merely the necessary adjuvant, not the cause of the secretion; it supplies the glands with the extra material they now require, the secretory nerves causing the gland-cells to utilize the increased supply.

The secretion of sweat may be induced in man, the cat, and the dog, though not in the horse, by the injection of pilocarpin. In this case the action is peripheral—that is to say, on the glands themselves—since it occurs when the sciatic nerves are cut previously to the injection.

As we have seen, secretion is ordinarily brought about by specific efferent nerves, and these originate in the central nervous system, from which the necessary secretory impulses are directly supplied. But secretion may also be readily induced by the stimulation of *afferent* nerves, as in the all-important case of a rise in the surrounding temperature. These facts lead at once to the belief that 'sweat centres' must exist in the central nervous system comparable to those of the respiratory and vascular mechanisms, though they have not as yet been so definitely localized. There seems to be no doubt that the spinal cord contains sweat centres. The existence of a similar centre in the medulla is less certain, though probable, since in some men perspiration over the face and neck results from merely smelling a pungent substance, such as curry-powder, and becomes profuse if the latter is introduced into the mouth.

The sweat-nerve supply to the fore and hind limbs passes out of the cord by means of the *rami communicantes* of the sympathetic system, and so reaches the brachial and sciatic plexus respectively; the sweat fibres for the head and neck are in the cervical sympathetic; those for the face in the horse, the muzzle in the ox, the snout in the pig, run in branches of the fifth pair of nerves. Division of the cervical sympathetic in the horse produces profuse sweating of the head and neck, limited to the side operated upon; this may be due to vaso-motor paralysis, though a different interpretation has been placed on it, viz., that the sympathetic carries inhibitory impulses to the sweat glands of the head, so that on division the secretory fibres act without opposition. In the ox Arloing has shown that division of the cervical sympathetic causes the muzzle on the same side to become dry; stimulation of the cut end of the nerve is followed by secretion, but this is not so when the nerve degenerates, though even then the glands respond to pilocarpin.

As previously stated, a high temperature favours the activity of the epithelium lining the sweat glands, for if the limb of a cat be kept warm a larger secretion of sweat is obtained on stimulating the sciatic than in a limb kept cold, in which latter stimulation of the sciatic may produce no secretion whatever. Further, if a cat in which one sciatic has been divided be placed in a hot chamber profuse secretion will occur on the foot-pads of the limbs not subjected to interference, while on the side on which the sciatic has been divided no sweating occurs. This is a further proof of the existence of a reflex mechanism, to which we have already drawn attention. It has been thought that the sweating which takes place at death is due to a dyspnœic condition of the blood and in many cases this may be so, but it is difficult to account for the profuse cold sweating in ruptures of such viscera as the stomach and intestines, or the localized hot sweating which is often so well marked in horses between the thighs immediately after they are destroyed. Thrombosis of both iliac arteries may occur in the horse, and a marked symptom of this trouble is the peculiarity in the accompanying sweating; the general surface of the body may sweat freely but not the hind-quarters. The cause of this peculiarity has not been worked out.

In comparing the sweat glands with the salivary we must be careful not to draw too close a parallel, for though in certain features they agree, in others they are very different; for instance in the horse pilocarpin produces, as in other animals, a profuse salivary flow, but, unlike its action on man, the dog, and cat, it has no effect whatever in producing sweating.

The peculiar breaking out into sweats which occurs in horses *after* work has no parallel in man; some animals will break out two and three times for hours afterwards, even after having been rubbed quite dry. This may be connected with the necessity for a discharge of body heat, since the internal temperature rises above the normal during work, in some cases, it is said, as much as 4° Fahr. to 5° Fahr., and remains so for some time afterwards. Another peculiarity in sweating of the horse is the patchy perspiration observed occasionally, such as a wet patch on the side or quarter which dries slowly, or may remain for days or weeks in a wet or damp condition. Finally, there is no drug, so far as we are aware, which produces sweating in horses; this is perhaps an explanation of the common use of nitre in veterinary practice, the kidneys being made to do the work of the skin.

The changes occurring in the secreting cells of the sudoriferous glands of the horse have been described by Renault. When charged the cells are clear and swollen, the nucleus being situated near their attached ends; when discharged they are smaller, granular, and their nucleus more centrally placed.

Sebaceous Secretion or **Sebum** is a fatty material formed in the sebaceous glands of the skin, which in the horse are freely distributed over the whole surface of the body. Though it is spoken of as a secretion, yet the process involved is not secretory, inasmuch as the cellular elements of the gland are not actively employed pouring out material, but are themselves shed after undergoing fatty metamorphosis. The greasy material thus produced saves the epithelium from the disintegrating influence of wet, keeps the skin supple, and gives the gloss to the groomed coat; from its greasy nature it assists in preventing the penetration of rain, and thereby saves to an extent undue loss of heat.

Dandruff.—The material removed from horses by grooming consists of a white or grey powder which can readily be moulded by pressure into a dough-like mass. It consists of epithelial scales, fat, largely in the form of lanolin, colouring matter, salts, and a considerable amount of silica and dirt, the two latter depending upon the cleanliness of the animal. The amount of dandruff lost in an ordinary grooming varies from 20 to 60 grains for clean horses, and 170 to 200 grains for very dirty animals. An analysis of dandruff from the horse gave the following composition :*

Water - - -	17·96	
Fat - - -	12·40	
Organic matter - -	56·22	containing 1·07 of urea.
Ash - - -	13·42	„ 2·45 of silica.
	100·00	

The fatty matter in the skin proves to be lanolin, the same as that found in the fleece of sheep; it explains the reason why horses living in the open should not be too freely groomed, and supports the prejudice which has always existed against this practice. It is evident that with free grooming the loss in fat alone is something considerable, and the animal exposed to chill. The amount of fat depends upon the diet; on hay alone there is very little in the dandruff, whilst on oats there is a considerable amount. The urea shown in the analysis is no doubt derived from the sweat.

Dandruff contains a colouring matter found to be chlorophyll, which has undergone modification by passing from the digestive canal to the skin. The use of this pigment is unknown, in fact, the horse is the only vertebrate in which chlorophyll has so far been found as a constituent of any cutaneous excretion.

In certain places, as in the prepuce, considerable quantities of **sebum** are found. The sebaceous secretion of the prepuce of the horse consists of 50 per cent. fat, and also contains calcium oxalate. The ear-wax and eyelid secretions are also of a sebaceous nature.

In the sheep a considerable quantity of fatty substance is found in the wool; it exists in two forms, (1) as a fatty acid united to potash to form a soap, and (2) a fatty acid combined with cholesterin instead of glycerin; the latter is known as lanolin, and is largely used as a basis for ointments. It is also found in hair, horn, feathers, etc. The fatty substance in the wool is known to shepherds and others as 'suint.' In merino sheep it may amount to more than one-half the weight of the unwashed fleece, but in ordinary weather-exposed sheep it may be 15 per cent. or less. The large amount of potash in unwashed wool is very remarkable; a fleece sometimes contains more potash than the whole body of the shorn sheep (Warrington).

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* 'Dandruff from the Horse, and its Pigment,' *Journal of Physiology*, vol. xv., 1893.

Respiratory Function of the Skin.—Certain vetebrates such as the frog can respire by the skin in the entire absence of lungs; in this way they absorb oxygen and excrete carbonic acid. Observations made on animals and men have demonstrated that similar changes occur through the skin, but on a very small scale.

Varnishing the skin rapidly causes death in rabbits, and more slowly in horses. Death is due to loss of body heat, and not to the retention of poisonous products as was at one time supposed. Bouley* states that horses shiver when varnished, and the surface of the body and the expired air become colder, the visible membranes respond by becoming violet in tint, and the animals die after several days. According to Ellenberger, if only partly varnished they do not die, but exhibit temporary loss of temperature, and show signs of weakness. The effect of varnishing the skin is to cause the capillaries to dilate, and so produce a great discharge of heat.

For absorption from the skin, see 'Absorption,' p. 258.

Pathological.

The chief pathological conditions of the skin are those due to parasitic invasion; they may produce widespread disease in all animals.

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* Colin's 'Physiologie.'

CHAPTER X

THE URINE

The urine is sometimes spoken of as a secretion, but this is not strictly correct; speaking broadly, we may say a secretion is something which is formed in a part for the purpose of being eventually utilized by the system. This does not apply to the urine, the chief constituents of which are not even prepared in the kidneys but only separated by them; moreover, the urine having once been formed is of no further use to the body and is excreted. An excretion, therefore, is something removed from the system as being no longer required, and the retention of which would be harmful. This removal is effected by the kidneys, which may in a sense be regarded as the filters of the body, regulating the composition of the blood by removing from it waste and poisonous products, and maintaining, as will be later explained, its proper degree of alkalinity.

In consequence of the discoveries which have been made of internal secretions, physiologists have forecast that the kidneys may yet be shown to take some important part in nitrogenous metabolism. This forecast is based on the fact that in the dog, with only one-quarter the normal amount of kidney substance left, double the normal amount of urea is excreted. We have seen how both nourishment and waste materials are poured into the circulation, and have studied several of the channels by which the latter are removed, viz., by the lungs, skin, and intestinal canal; we have now to examine the last excretory path, viz., the kidneys.

The vascular arrangements of the kidney are intimately connected with the function of the organ. The renal artery is short, it comes off close to the posterior aorta, and the pressure within it is practically the pressure in that vessel; the pressure in the renal vein on the other hand is low, nearly as low as that in the posterior vena cava. It will be observed that the same amount of blood-pressure as is required to fill the vessels of the lumbar region and hind limbs is expended on driving the blood through the kidneys.

At every increase in the amount of blood in the kidney the organ swells, at every decrease it contracts. These movements on the part of the kidney have been carefully studied by means of Roy's *oncometer*. An oncometer is a metallic capsule in which the living kidney is enclosed, and so arranged that the expansion and collapse of the organ can readily be detected. A tracing given by the use of this instrument shows that the volume of the kidney is affected by every beat of the heart, and even the respiratory undulations in the blood-pressure.

Structure of the Kidney.—The kidney consists of a central part, the medulla, surrounded by an external part, the cortex; the boundary of the two is easily visible in a sliced kidney. The branches of the renal artery break up at the boundary of the cortical and medullary portions; the cortex of the kidney is the essential secreting region, and it is here that the *Malpighian tufts* or *capsules* are found. These consist of small balls of capillaries, the *glomeruli*, derived from the renal artery; the artery entering the Malpighian tuft is larger than the vein leaving it, the result is that a high blood-pressure is maintained in the glomerulus. The vessel which supplies these tufts also sends branches to form a plexus around the *uriniferous tubules;* these branches do not enter the Malpighian body. The whole glomerulus is contained in a capsule in which it is suspended by its afferent and efferent vessel; when the vessels are dilated the tuft fills the capsule, when they are collapsed there is a space between them (Fig. 65).

The minute vein or efferent vessel leaving the tuft breaks up into capillaries around the uriniferous tubule; thus the blood in the plexus of capillaries around the tubule is derived from two sources, viz., from the tuft, and directly from the renal artery.

The capsule of Bowman which surrounds the tuft is lined by cells resembling the epithelioid plates seen in capillaries; they are flat polygonal cells containing a nucleus. The capsule is practically the dilated beginning of a uriniferous tubule, and the latter is continued from the capsule, taking a course of extraordinary complexity in order to reach the pelvis of the kidney; further, the cells found in the tubule are no longer the flat polygonal cells of the capsule, but a something special to the tubule and even to different parts of it.

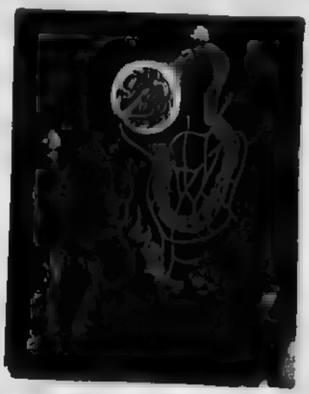

FIG. 65.—DIAGRAM SHOWING THE RELATION OF THE MALPIGHIAN BODY TO THE URINIFEROUS TUBULES AND BLOODVESSELS (KIRKE, AFTER BOWMAN).

a, An interlobular artery; *a'*, branch of artery passing into the glomerulus; *c*, capsule of the Malpighian body forming the commencement of, and continuous with *t*, the uriniferous tube; *e'e'e'*, vessels leaving the tuft, forming a plexus *p* around the tube, and finally terminating in *e*, a branch of the renal vein.

If we briefly follow the course of a uriniferous tubule (Fig. 66), it is found that on leaving the capsule it becomes twisted in the cortex forming the *convoluted tube;* it then forms a *spiral tube*, and leaving the cortex runs straight into the medulla, forming the *descending limb of Henle;*

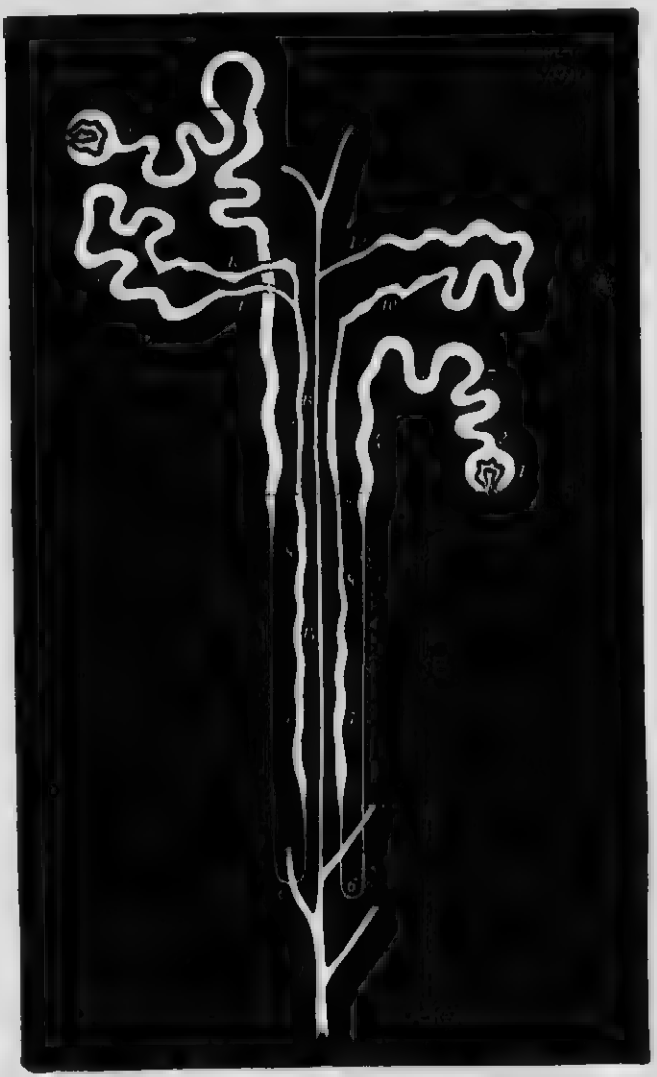

FIG. 66.—DIAGRAM OF THE COURSE OF THE URINIFEROUS TUBULES (KLEIN AND NOBLE SMITH).

A, Cortex of kidney; *a*, subcapsular layer not containing glomeruli; *a′*, inner structure of cortex also without glomeruli; B, boundary layer of medulla; C, papillary part of the medulla; 1, Bowman's capsule of the glomerulus; 2, neck of capsule; 3, proximal convoluted tube; 4, spiral tube; 5, descending limb of Henle; 6, loop of Henle; 7, thick part of ascending limb; 8, spiral part of ascending limb; 9, narrow ascending limb in the medullary ray; 10, the irregular tubule; 11, distal convoluted tube; 12, curved collecting tube; 13, straight collecting tube; 14, collecting tube of boundary layer; 15, large collecting or discharging tubule of papillary layer.

it now makes a sharp turn, the *loop of Henle*, and travels back to the cortex, in the same way that it left, by the *ascending limb of Henle*. The descending limb is straight and narrow, the ascending limb is wavy in character and larger. Having reached the cortex the ascending limb becomes distinctly wider and twisted, forming the *zigzag* or *irregular tubule ;* from this a tubule is continued which resembles in its contortions the first convoluted portion ; it is termed the *second convoluted tubule*. This now leaves the cortex and enters the medulla as a straight tube, known as the *collecting tube ;* it runs towards the apex of the pyramid and joins other collecting tubes; by so doing it becomes larger, and on reaching the apex is known as a *discharging tube* or *duct of Bellini*.

The epithelial cells lining the tubules are not of the same character throughout; broadly, they may be divided into a striated cell staining readily, and a clear transparent cell staining with difficulty. The first epithelium is suggestive of secreting cells, the latter, on the other hand, possesses more the characteristics of the epithelial lining of ducts.

The amount of blood passing through the kidney is something very considerable; it has been calculated that in 24 hours 146 lbs. of blood will pass through the kidneys of a dog weighing 66 lbs.

Vascular Mechanism.—The vascular arrangements of the kidney are under the control of a rich supply of vaso-constrictor nerves, while dilator nerves are also known to exist. If the general blood-pressure be constant, dilatation of the renal vessels means an increased secretion of urine, while constriction of the vessels means a reduced secretion. An increase in the general blood-pressure produces an increase in the amount of blood in the kidney, and this is rendered evident by the swelling of the organ in the oncometer and an increased production of urine. If the increased general blood-pressure is accompanied by a *constriction* instead of a dilatation of the small arteries of the kidney, such for instance as when the vaso-constrictor nerves are stimulated, then the increased blood-pressure cannot lead to increased secretion, but on the contrary the amount of urine becomes less and the kidney *shrinks*. A fall in general blood-pressure, such as is caused by dividing the spinal cord, brings about a reduction in the flow through the kidney, and the blood-pressure becomes so low that the secretion of urine is entirely suspended. It is thus evident that the vaso-motor influence over the kidney is of the greatest importance, and largely regulates the amount of urine manufactured. If the renal vein be obstructed, the pressure of blood in the kidney rises, but no urine is secreted; evidently therefore an increased flow of blood through the kidney is as essential to secretion as is increased blood-pressure.

Two **theories of urinary secretion** have hence been put forward, one being based on the physical conditions which are favourable in the kidney to filtration, while the other is based on the supposition that the cells are secretory. It is obvious that there are two portions of the kidney engaged in the manufacture of urine, viz., the glomerular and the tubular. In the former the conditions for filtration from the bloodvessels of the tuft into Bowman's capsule exist, yet the experiment of obstructing the renal vein, referred to above, has impressed on physiologists the influence of the activity of the endothelial cells of the glomerulus, for if filtration pure and simple could obtain water from the Malpighian tufts, more urine should have been secreted *immediately*, though not continuously, after ligaturing the renal vein than before. As a matter of fact we know that secretion ceases.

The evidence of secretory activity in the tubules of the kidney is based on the following experiment. If sulph-indigotate of soda be injected into the blood of the dog, within a short time the urine acquires an intensely blue colour, though the blood may be only slightly affected. If the kidney be removed and examined, all parts but the Malpighian bodies are found stained blue. In order to determine what portion of the tubule excretes the dye it is necessary to stop the secretion in the glomeruli, otherwise the dye gets carried through the whole length of the tubule. In order to stop glomerular secretion the spinal cord is divided in the neck, the blue colouring matter injected, and the kidney examined. The blue is now found in the cortex only, and within the striated epithelial cells of the first and second convoluted tubes, where the indigo may be seen in granules. From this experiment it is clear that the cortical tubules elected to turn out the indigo, while the medullary tubules were unable to effect this, from which it is judged that a specific secretory activity of these cells is shown for indigo, and it is assumed that a similar function may be exercised towards other bodies, for instance, urea and the other constituents of the urine.

Stating these points briefly in connection with secretion they amount to this, that in the glomeruli the water of the urine, and perhaps the salts, are passed out chiefly as the result of varying glomerular blood-pressure, while in the tubules the organic matter is excreted as the result of a distinctly secretory activity of their cells. These substances are carried along by the fluid which trickles down the tubules into the pelvis from the kidney and so becomes urine. Under pathological conditions the glomeruli admit of the exit of both albumin and sugar.

The secretion of proteid in the tuft and its reabsorption in the tubule was at one time believed to be true, but inasmuch as no proteid is found in the normal urine of any animal, it is safe to assume that in an undamaged state the epithelial cells of the glomerulus allow none to pass.

There are no secretory nerves to the kidney; the influence of the nervous system is confined to its action on the bloodvessels. The action of diuretics has been studied in connection with the question of urinary secretion, and most observers find that though these determine a greatly increased flow of blood to the kidneys, yet they also exert a directly stimulating effect on the secretory cells.

The function of the cells of the tubules does not end with the removal from the blood of the substances presented to them; they are also capable of originating material on their own account. Thus the union of glycine with benzoic acid, resulting in the formation of hippuric acid, takes place in the cells of the tubules, and observations have shown that providing the benzoic acid be presented to it, the kidney is capable of providing the needful glycine. It can hardly be doubted that what is true of glycine and benzoic acid may also be true of other substances, and that transformations may occur in the cells leading to the production of colouring matters, etc., our knowledge of which is at present obscure.

The **Composition of the Urine** depends upon the class of animal; in all herbivora, with certain minor differences, the urinary secretion is much the same: not so with omnivora or carnivora which possess a distinctive urine, especially the latter. When herbivora live on their own tissues, as during starvation, they become carnivora and their urine alters completely in character, corresponding now to the urine of flesh feeders; the young of herbivora, if still sucking, have a urine possessing much the same characteristics as that of carnivora. But apart from this general statement, it is necessary to point out that in animals of the same class the composition of the urine may vary within very wide limits, depending upon several causes, of which diet is, perhaps, the most important.

Urine consists of:

Water.	
Organic matter	Nitrogenous end-products: urea, uric acid, hippuric acid, creatine, creatinine. Aromatic compounds: benzoic acid, ethereal sulphates of phenol, cresol, etc. Colouring matter and mucus.
Salts	Sulphates, phosphates, and chlorides of sodium, potassium, calcium, and magnesium.

The **Nitrogenous Substances** taken up into the blood, either from the disintegration of proteids in the digestive canal or from the metabolism of the tissues, supply the total nitrogen of the urine. A distinction is made between the nitrogen from without, viz., that supplied by the food, and the nitrogen from within, viz., that from the tissues, and this is more especially of interest in connection with urea and uric acid.

The total nitrogen of the urine consists of:

1. Urea nitrogen.
2. Uric acid nitrogen.
3. Ammonia nitrogen.
4. Creatinine nitrogen.

Speaking generally, the nitrogen varies directly with the amount of proteid taken as food.

Urea.—It is by no means decided how urea is produced. It must presumably arise from the disintegration of proteids, derived either from proteid food or proteid tissues. As the result of their destruction it is extremely probable that ammonia compounds are formed which are discharged into the blood, and are then subsequently converted into urea in some organ, which is probably the liver. Some suppose that the proteids undergo hydrolytic cleavage with the formation of amido-bodies, such as leucine, tyrosine, aspartic acid, glycocoll, etc., and that these bodies undergo oxidation in the tissues yielding ammonia, carbonic acid, and water. The ammonia and carbonic acid unite to form ammonium *carbamate*, which is carried to the liver, and by the loss of a molecule of water is readily converted into urea. The oxidation of the amido-bodies is essential as a preliminary step towards urea, in order to get rid of some of the carbon they contain; in amido-bodies this is in excess of the nitrogen, whereas in urea the reverse is the case. It seems fairly clear that the nitrogenous waste leaves the muscles as ammonia compounds, and in this form the nitrogen of the proteid food may be found in the portal vein, the blood of which contains three to four times as much ammonia compounds as does arterial blood. If the blood of the portal vein be experimentally compelled to pass into the posterior vena cava without circulating through the liver, the ammonia compounds in the arterial blood become equal in amount to those in the portal blood. The ammonia in the blood is considered by some to be in the form of carbonate; by others, and perhaps more generally, as carbamate, though ammonium carbamate is readily produced from the carbonate by the loss of one molecule of water. The subsequent disposal of the ammonia compounds is evidently by means of the liver, this gland standing between the portal and systemic circulation, and converting the poisonous ammonia compounds into the less poisonous urea.

In the urine the urea exists in a free and uncombined state, though it is capable of forming salts with acids (Fig. 67). It is a substance very soluble in water.

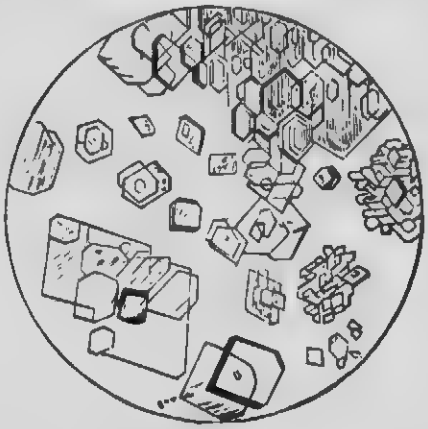

FIG. 67.—CRYSTALS OF NITRATE OF UREA (FUNKE).

The proportion of urea in urine varies dependently on the nature of the diet. As a rule the larger the amount of nitrogen in the food the more urea excreted, but this is not invariable, for some observers have stated that on a diet consisting principally of hay more urea is excreted than on one of oats and hay. Urea was at one time considered to be a measure of the amount of work performed by the animal body, but this view has long been known to be wrong, though there can be no doubt that under the influence of work rather more urea may be excreted than during rest.

Judging from our observations on the horse, great variation in the amount of urea may be met with even when the conditions as regards diet, rest and work are identical. It is probable that this applies also to other animals. The percentage of urea present in urine may broadly be stated to vary between 3 and 4 per cent., but it is obvious that the percentage present is influenced by the total secretion for the twenty-four hours. If this is small in amount, the percentage is higher than when an average production of water occurs.

Creatinine has been regarded as another source of urea, but the physiological history of this substance is imperfectly known. In flesh-feeding animals part of it, no doubt, is derived from the food, while another portion is produced within the body, probably originating from the metabolism of muscle. Though the conversion of creatinine into urea may be brought about as a laboratory process, there is no definite proof that the conversion occurs in the body; if creatine be injected into the blood it does not lead to an increase of urea but of creatinine. It is possible that under physiological conditions creatine before it leaves the muscles may undergo a further change, being decomposed into urea and sarcosine, the latter passing to the liver and there being converted into ammonium carbonate and subsequently into urea.

Uric Acid.—The origin of uric acid is not clearly determined in mammals. In birds it is known to be formed in the liver from ammonia compounds, and probably from lactic acid. In mammalia it is known that in herbivora the amount of uric acid is extremely small, or this substance may be even entirely absent; in carnivora and omnivora it is present, though only in a small proportion of the total nitrogen excreted. The influence of diet in flesh feeders is very marked, meat causing a rise in the uric acid output, while cellular organs, such as liver and sweetbreads, produce a still greater rise; this fact has afforded a clue to the probable origin of uric acid in the body, viz., from the nucleo-albumins and nucleins, both of which largely exist in the cellular organs. Pathologically there is an increase in uric acid in the disease known as leucocythæmia, in which a great increase in the white blood-corpuscles occurs. These corpuscles contain a quantity of nuclein, and the work of Emil Fischer has shown the close chemical relationship between the nitrogenous bases so easily obtained by the decomposition of nuclein—the *purin*[*] bases—and uric acid. The purin bases are hypoxanthine, xanthine, and adenine, and from these uric acid may arise by the process of oxidation. For example, one atom of oxygen allied to purin ($C_5H_4N_4$) gives rise to hypoxanthine ($C_5H_4N_4O$), two atoms of oxygen to xanthine ($C_5H_4N_4O_2$), and three atoms of oxygen added to purin lands us finally in uric acid ($C_5H_4N_4O_3$).

If hypoxanthine or uric acid be given to dogs the uric acid is not increased; if adenine be given the animal dies from suppression of urine and crystals of uric acid block the renal tubules. It is evident that very little is known of the subject of uric acid formation. Even the seat of production is not definitely ascertained, though the liver will probably be found to play no small part in the process, as it is already known to do in the case of birds. The spleen has been pointed to as a probable seat, though possibly it is not relatively more so than other lymphoid tissues.

As previously stated, the production of uric acid is affected by diet, being largest on animal food and smallest on vegetable. The acid is therefore present in the dog fed on meat and in the pig, but entirely absent, so far as our observations go, in the horse in health, and probably in all herbivora unless still suckling at the mother. It is important to note that during sickness, especially when there is fever and the animal is living on its own tissues, uric acid may be readily found in the urine of herbivora. The explanation is simple: the animal for the time being is practically carnivorous.

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[*] Purin is the name given by Fischer to the nucleus common to the uric acid group of substances from which, by simple transformations, the several members of the group may easily be obtained.

Uric acid does not occur free in the urine, but in combination with soda and potash. Its crystalline formation is shown in Fig. 68; it is a substance very insoluble in water, but soluble in alkaline solutions.

The *ammonia salts* present in urine are an index to the neutralization of acids in the body. The acid substances are produced as the result of metabolism; when they are in excess there is an increase in the ammonia of the urine, the formation of ammonia in the muscles being the natural protection of the body against acid poisoning. When, as occurs in herbivora, there is already an excess of alkali in the diet, a sufficiency of bases is present to neutralize the acid, and ammonia is absent from the urine. With flesh feeders the amount of ammonia is kept at a minimum owing to its poisonous nature; on a vegetable diet it all disappears from the urine, being converted into urea.

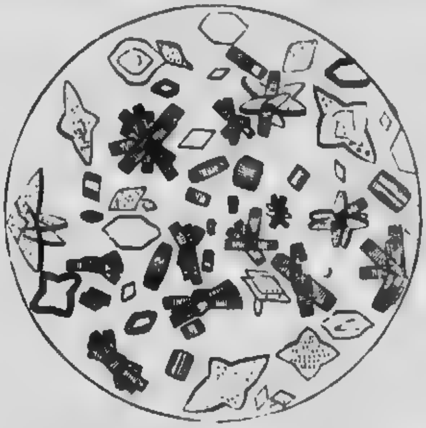

FIG. 68.—CRYSTALS OF URIC ACID (FUNKE).

The injection of dilute mineral acid into the veins of a dog does not alter the reaction of the blood, but the ammonia is increased as a natural protection and appears in the urine, with a resulting decrease in the urea. A similar injection of dilute mineral acid in herbivora reduces the alkalinity of the blood, after having used up the store of vegetable alkaline salts. In consequence of the reduced alkalinity the carrying power of the blood for carbon dioxide is reduced; it is retained in the tissues, and gives rise to symptoms which may prove fatal. If ammonium carbonate be given by the mouth, it does not appear as such in the urine, but as urea.

Hippuric Acid.—This acid, characteristic of the urine of the herbivora, may arise in two or three different ways. It is known that hay, grass, and grains, contain in their cuticular covering a substance which yields hippuric acid in the body; if these foods be extracted with caustic potash the hippuric-acid-forming substance is removed, and if animals are fed on forage so treated no hippuric acid is formed in the body; even, it has been said, if the husk be removed from grain the latter is incapable of giving rise to hippuric acid.

The chief source of hippuric acid in the herbivora is from the above hippuric-acid-yielding body. Benzoic acid is derived from various aromatic combinations contained in plants, and this combined with glycocoll, derived from the decomposition of proteid substances, yields hippuric acid. The synthesis occurs in the kidney, and is brought about by the cells of the gland in conjunction with the oxygen of the red corpuscles. Outside the body the synthesis may be produced by using ground-up kidney tissue mixed with blood, and kept at the body temperature. It is probable that the active agent in the synthesis is an enzyme. A second source of hippuric acid is the aromatic (benzoic) products formed in the intestinal canal as the result of the putrefaction of proteids; lastly, it is believed that hippuric acid may be formed from the aromatic residues of tissue proteids.

Hippuric acid never exists in the free state in the urine, but either as hippurate of lime or potash, probably the former. Crystals of hippuric acid are shown in Figs. 69 and 70. The amount of hippuric acid excreted varies with the diet; it is increased by using meadow-hay and oat-straw, and decreased by using clover, peas, wheat, oats, etc.; as the urea rises the hippuric acid falls.

Liebig many years ago stated that benzoic acid was found in the urine of working horses, and hippuric acid in the urine of those at rest. Our observations show that hippuric acid is generally found in the urine of working horses, and seldom found in the urine of horses at rest—in fact, the reverse of Liebig's view. Owing to its easy and

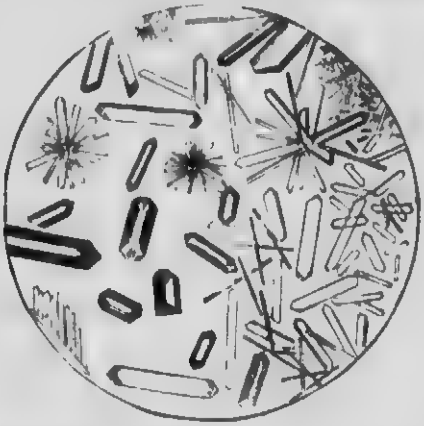

Fig. 69.—Crystals of Purified Hippuric Acid (Funke).

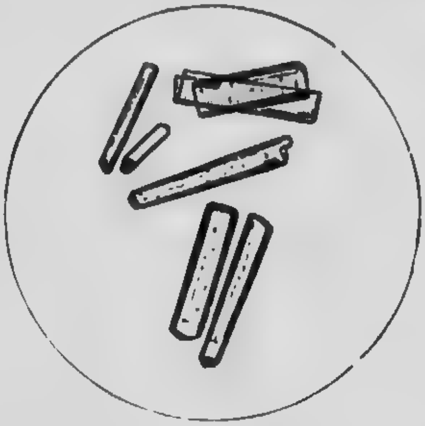

Fig. 70.—Crystals of Impure Hippuric Acid.

rapid fermentative decomposition hippuric acid is rarely to be found in urine twenty-four hours old; in fifty-four specimens we only found it eight times. This decomposition may be prevented by the addition of a slight excess of milk of lime, and then boiling the freshly voided urine.

Benzoic Acid is the antecedent of hippuric. As just mentioned, it is derived from the benzoic-acid-forming substances in vegetable food; its crystalline formation is show in Fig. 71.

Sulphuric Acid in the urine of carnivora and omnivora is almost wholly derived from the decomposition of proteid bodies undergoing digestion, and its amount is employed as a measure of proteid disintegration in the system. The sulphur is derived from the sulphur of the proteid body, and the acid is united with *indol*, *phenol*, *skatol*, *cresol*, all of which are products of proteid disintegration in the intestinal canal. In herbivora indol, phenol, and skatol may be derived from the benzene compounds in food, so that the amount excreted is no measure of proteid disintegration. Phenol, skatol, and cresol are poisonous bodies; part of them are got rid of by the fæces, part are absorbed into the blood, and after oxidation are conjugated with sulphuric acid and eliminated by the urine. By this conjugation the poisonous aromatic compounds are rendered harmless.

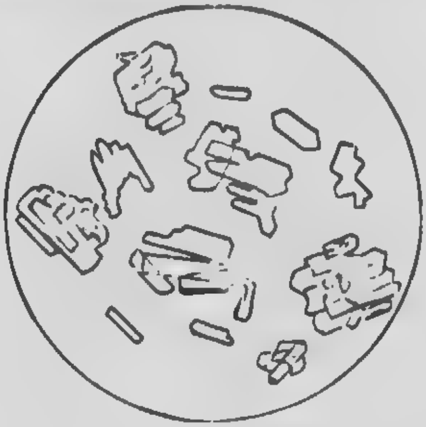

FIG. 71.—CRYSTALS OF BENZOIC ACID.

From the conjugation between indol and sulphuric acid *indican* is produced, which may be made to yield indigo, a substance common in the urine of herbivora. From the conjugation between phenol and sulphuric acid a colouring matter is formed which is found in stale urine; phenol-sulphuric acid undergoes oxidation in the presence of the air, and yields *pyrocatechin*, to which the brown colour in the stale urine of the horse is due.

Some of the indol and skatol may be united with glycuronic acid, a substance co-related to dextrose, and often present in the urine of the dog. It exerts a reducing action on salts of copper.

Oxalic Acid in combination with lime is constantly found in the urine of herbivora; its deposit presents a characteristic microscopical appearance (Fig. 72). In dogs it has been produced in considerable quantity by feeding on uric acid; its origin in the herbivora is doubtless from the oxalates contained in the food.

The **Colouring Matter** of the urine is not yet completely worked out. The chief substance is *urochrome;* this is probably an oxidation product of urobilin, as on suitable treatment a pigment is obtained which gives a spectrum identical with urobilin. Urobilin is not found in normal urine, but there is present a chromogen, or another substance, which yields urobilin. The origin of urobilin is from bile pigment; the stercobilin formed in the intestines is identical with it.

The **Inorganic Substances** found in the urine are calcium, magnesium, sodium, and potassium, existing in the form of chlorides, sulphates, phosphates, and carbonates. The origin of these salts is from the food taken into the body, but mainly from metabolic processes occurring in the tissues. The nature and amount of the salts vary with the class of animal and the character of the food. In the urine of the horse potassium salts predominate, sodium and magnesium are present in small amounts, phosphates are practically absent, while sulphates and chlorides are in considerable quantity. It has been found that in ruminants the calcium salts are mostly excreted with the fæces, whereas in the horse they principally pass through the kidneys. It is certain that phosphates, which form such a prominent feature in the urine of carnivora and omnivora, are in the horse almost wholly excreted by the intestines.

Calcium.—More lime exists in the urine of the horse than is soluble in an alkaline fluid, so that both suspended and dissolved lime exists; the former increases with the age of the urine, owing to the development of ammonia, until nearly the whole of the lime is precipitated. The lime exists in combination with oxalic, carbonic, hippuric, and sulphuric acids; all these combinations do not necessarily exist in one specimen of urine, the salts formed depending

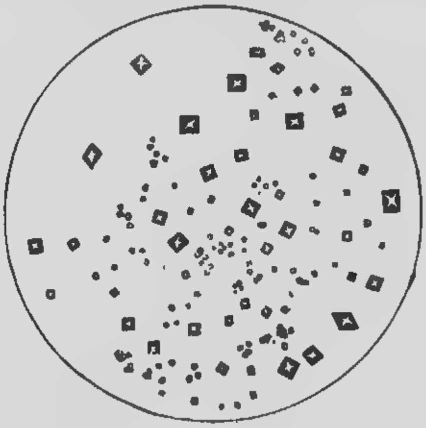

Fig. 72.—Crystals of Oxalate of Lime (Funke).

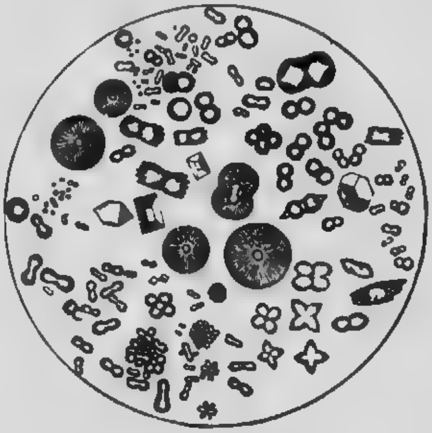

Fig. 73.—Crystals of Carbonate of Lime (Funke).

on the varying relative amounts of the acids formed in metabolism. The amount of lime in the food does not influence the elimination through the kidneys, but more lime is found in the urine of horses at work than of those at rest. Oxalate and carbonate of lime crystals are common microscopic deposits in the urine of the horse (Figs. 72 and 73).

Under any condition the urine of a healthy horse is turbid from suspended lime; this may be got rid of on the addition of acid with profuse evolution of gas, while a clear transparent urine results.

Magnesium in the urine is also suspended and dissolved, the amount which is suspended being increased by the ammonia generated in the urine on standing.

Potassium exists largely in the urine of herbivora, derived from the potash of the food; it forms numerous combinations, the one with carbonic acid being the cause of the fixed alkalinity of the urine in the horse. There is more potash found in the urine of horses at rest than of those at work, which is explained by the considerable amount of potassium excreted with the sweat. **Sodium** only exists in the urine of herbivora in small quantities, which is due to the fact that very little sodium is found in vegetable food.

Sulphuric Acid in its organic combinations has been dealt with previously; the inorganic sulphur is combined with alkalis as ordinary salts.

Chlorine is supplied by the chlorides of the food. The proportion of chlorides in the food of herbivora is not very high; the amount excreted by horses, combined with sodium, was found by us to equal a daily excretion of 85¼ grains of common salt. Salkowski places it much higher, viz., about ¾ oz. daily.

Phosphoric Acid, though existing largely in food such as oats, passes off almost wholly by the alimentary canal; sometimes only traces are to be found in the urine of herbivora, at others the amount is marked, but never considerable. Work does not influence its production. In the urine of carnivora the phosphates are an important constituent. They exist in the urine in two forms, viz., alkaline phosphates, such as phosphate of sodium or potassium, and earthy phosphates, such as phosphates of calcium and magnesium; these triple phosphates are common as a microscopical object in the decomposing urine of the horse, though trifling in actual amount (Fig. 74). The phosphates are derived from the food and tissues. According to Munk, if there is an abundance of lime salts in the diet, as in vegetable food, the phosphates are not eliminated to any extent by the kidneys, for the reason that they combine in the intestinal canal with lime and magnesia and pass off by that channel; if, on the other hand, there is but little lime and magnesia in the intestines, the phosphates are united to soda and potash, pass into the blood, and are eliminated by the urine.

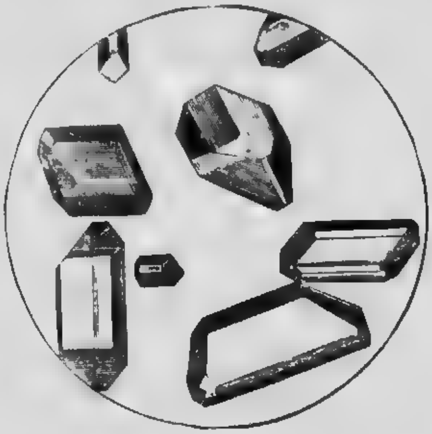

FIG. 74.—CRYSTALS OF TRIPLE PHOSPHATE (FUNKE).

Ammonia.—Free ammonia exists in the urine of the horse. It may be owing to ammoniacal fermentation in the bladder, but it is quite certain that perfectly fresh urine may give marked evidence of the presence of free ammonia. On standing a short time outside the body, especially in summer weather, the urea decomposes and carbonate of ammonium is largely formed.

The **Reaction** of the urine of herbivora is alkaline, the alkalinity being due to carbonate of potash. The urine of all vegetable feeders is alkaline, owing to the excess of alkaline salts of organic acids contained in the food, such as malic, citric, tartaric and succinic. During their passage through the body these salts are converted into carbonates, and appear as such in the urine, where they produce considerable effervescence on the addition of an acid. The nature of the food influences the reaction, for if hay be withheld from the diet, the urine of the horse may be rendered acid by feeding entirely on oats; this is probably due to the formation of acid phosphates from the food. A considerable quantity of the alkalinity present in the stale urine of the horse is due to the exceedingly rapid fermentative change which occurs in it on standing, leading to the breaking up of part of the urea and the formation of ammonium carbonate.

In the dog the urine is acid, due to the acid phosphate of soda, and not to any free acid; no free acids exist in the urine of any animal. In the pig the reaction is either acid or alkaline, depending on the diet: an animal diet producing an acid and a vegetable diet an alkaline urine.

Urine of the Horse.

Specific Gravity.—This varies considerably dependently on the diet and the amount of dilution. The mean of a large number of observations was 1036, the highest registered was 1050 and the lowest 1014.

The Quantity of urine is liable to very considerable variation depending on the season and the diet; the more nitrogen the food contains the larger the amount of water consumed and the greater the bulk of urine excreted. The mean of a large number of observations was 8½ pints (4·8 litres) in 24 hours, the diet being moderately nitrogenous, but in individual instances very much more than this may be met with, viz., 12, 15, or even 20 pints (11·3 litres).

Horses at work excrete less urine than those at rest, probably owing to the loss by the skin. In winter, owing to the reduced action of the skin, more urine is excreted than during summer.

The *Odour* of urine is said to be due to certain aromatic substances of the phenol group. Perfectly fresh urine has commonly a most distinct though faint smell of ammonia. This may be due to fermentative changes occurring in the urea before the urine is evacuated.

The normal fluid is always turbid, some specimens more so than others; very rarely is it clear, and then only for a short time. The turbidity is due to the amount of suspended carbonate of lime and magnesia it contains; as the urine cools, particularly if it undergoes ammoniacal fermentation, the amount of turbidity becomes intense.

The *Consistence* of the fluid depends upon sex, and perhaps on the season. It is certain that some mares excrete a glairy tenacious fluid which owing to the amount of mucin it contains can be drawn out in strings; it is very common to find it as thick as linseed-oil, and very rare to find it fluid and watery. During œstrum the urine is of the consistence of oil. On a diet of oats and no hay, we have seen the urine so mucinous as to pour like white of egg.

The *Colour* of urine is yellow or yellowish-red, rapidly turning to brown, the dark tint commencing on the surface of the fluid and gradually travelling into its depth. The cause of the colour on standing is due to the oxidation of pyro-catechin (see p. 301).

The *Total Solids* consist of organic and inorganic matter, of which on a mixed diet 5 ozs. are organic and 3 ozs. inorganic; the quantities are liable to great variation, sometimes being found greatly in excess of that mentioned. The total solids are considerably affected by the diet; E. Wolff* found that when he reduced the hay and increased the corn ration the solids in the urine decreased, whereas on a diet consisting principally of hay and but little corn the solids increased.

The composition of the mineral solids is given in the following table by Wolff. In every 100 parts of salts there are found:

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* Ellenberger.

Potassium	36·85 per cent.
Sodium	8·71 „
Calcium	21·92 „
Magnesium	4·41 „
Phosphoric acid	—
Sulphuric „	17·16 „
Chlorine	15·36 „
Silicic acid	·32 „

In the following table are given the results obtained by us in the examination of the twenty-four hours' urine of horses at rest and work:*

	Rest.	*Work.*
Quantity	8·69 pints	7·88 pints
Specific gravity	1036	1036
Total solids	8·11 ozs.	8·19 ozs.
Organic solids	5·15 „	5·37 „
Inorganic solids	2·94 „	2·82 „
Urea	3·47 oz.	
Ammonium carbonate as urea	·46 „	
Ammonia	·09 „	·19 „
Benzoic acid	·23 „	
Hippuric acid		·55 „
Phosphoric anhydride	·04 „	·06 „
Sulphuric „	·87 „	·54 „
Other sulphur compounds	·26 „	·27 „
Chlorine	1·12 „	·77 „
Calcium oxide	·12 „	·06 „
Magnesium oxide	·10 „	·09 „
Potassium „	1·29 „	·95 „
Sodium „	·09 „	·06 „

Salkowski† examined the urine of the horse, and gives the following as the composition of one specimen:

Water	8·5 pints	Phenol	87·89 grains
Organic solids	6·25 ozs.	Organic sulphur	208·69 „
Ash	1·60 „	Inorganic „	85·77 „
Urea	3·25 „	Phosphoric acid	8·40 „
Ammonia	5·58 grains	Lime	88·50 „
Hippuric acid	·49 oz.	Sodium chloride	·87 oz.

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[*] 'Chemistry of the Urine of the Horse,' *Proceedings of the Royal Society*, vol. xlvi., 1889.

[†] Ellenberger's 'Physiologie.'

In the following summary of the urine of animals other than the horse, the main facts are those given by Tereg.*

The Urine of the Ox.

The urine of the ox is much the same as that of the horse, excepting that it is secreted in larger quantities, 10 to 40 pints; the difference mainly depends upon the amount of nitrogenous matter in the diet, for it has been shown that the more nitrogen a diet contains the larger the amount of water consumed. The fluid is clear, yellowish, and of an aromatic odour; it is of a lower specific gravity than that of the horse, 1007 to 1030 (in milch cows, according to Munk, 1006 to 1015), owing to the larger amount of water secreted.

The nitrogenous matter found in the urine is mainly represented by urea and hippuric acid, and the amount varies according to the diet. On a diet of wheat straw, clover hay, beans, starch, and oil, the amount of urea may be 4 per cent.; while on one of oat straw and beans it may fall to less than 1 per cent. When the urea is high, the hippuric acid is low, and *vice versa.* The largest amount of hippuric acid is produced by feeding on the straw of cereals, the smallest is furnished by feeding on leguminous straw, whilst a medium amount is produced by feeding on hay.

The urine of ruminants contains less aromatic sulphur compounds than that of the horse, and more of the inorganic sulphur; like the horse, the phosphates are either absent or only occur in small amounts.

The following table by Tereg shows the composition of the urine of the ox on different diets; the observations extended over four months:

	lbs.	*lbs.*	*lbs.*	*lbs.*
Total quantity of urine -	26·02	31·17	29·98	[illegible]·32
" " dry matter -	1·71	1·51	1·40	1·14
" " ash - -	·88	1·01	1·03	·66

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* Ellenberger's 'Physiologie.'

Calves still suckling excrete an acid urine which is rich in phosphates, uric acid, creatinine, and a peculiar substance known as allantoin; it is poor in urea, and, according to Moeller, contains hardly 1 per cent. of solids.

The Urine of the Sheep.

This has an alkaline reaction, a specific gravity 1006 to 1015, and the amount excreted varies from ·5 pint to 1·5 pints. Tereg gives the following percentage composition of a sample:

Water	86·48
Organic matter	7·96
Inorganic matter	5·56

The organic matter contained:

Urea	2·21
Hippuric acid	3·24
Ammonia	·02
Other organic substances	2·07
Carbonic acid	·42
	7·96

The inorganic matter contained:

Chlorine	1·05
Potassium chloride	1·84
Potassium	2·08
Lime	·07
Magnesia	·20
Phosphoric acid	·01
Sulphuric "	·24
Silica	·07
	5·56

In sheep urea and hippuric acid stand in the proportion of 2 to 3, whereas in cattle on the same diet the proportion is 2 of urea to 1·1 of hippuric acid.

The food most productive of hippuric acid in the horse is old meadow hay, whilst *new* meadow hay has this effect on sheep. It will be observed from the table how rich the urine of the sheep is in hippuric acid.

In sheep there is very much more magnesia than lime in the urine, consequently the reverse obtains in the fæces of this animal.

The Urine of the Pig.

This resembles that of carnivora, but its composition depends on the character of the food. The specific gravity is 1003 to 1025. It is either acid or alkaline; the amount excreted varies between 2½ to 14 pints, and it contains uric acid, hippuric acid, xanthine, guanine, and much urea.

In the following analysis of the urine the diet consisted of peas, potatoes, and sour milk:

Total urine - - -	7 pints
Sp. gr. - - -	1018
Dry substance - -	2·768 per cent.
Total nitrogen - -	·604 "
Ammonia - - -	·024 "
Ash - - - -	1·284 "

The ash largely consists of phosphates and potassium salts, a moderate amount of magnesium, and very little sodium or calcium.

The Urine of the Dog.

It is impossible to give the composition of the urine of the dog, as the amount of constituents secreted varies considerably in dependence upon the nature of the diet.

The urine is acid in reaction on a flesh diet, the acidity being due to acid phosphate of soda; on a vegetable diet it may be alkaline. The amount excreted is from ¾ to 1¾ pints daily, but varies with the size of the animal and the nature of the diet; the specific gravity is from 1016 to 1060 depending on the diet; the colour is pale yellow to straw yellow; the urea varies from 4 per cent. to 6 per cent. On an animal diet uric acid is excreted, but disappears on giving vegetable food; hippuric acid in small quantities appears with fair regularity; indican and phosphoric acid are well-marked constituents, and a substance known as glycuronic acid may be found which exercises a reducing action on salts of copper. The presence of bilirubin in the urine of the dog has been noted by Salkowski (see p. 221).

As an illustration of the variation of the dog's urine dependently on the nature of the diet, we may take an example from a long series of experiments by Bischoff and Voit.

On a diet consisting of meat ·57 lb., starch ·71 lb., salts 77·5 grains, a specimen of urine gave the following composition:

Amount	·44 pint
Sp. gr.	1049
Urea	326·6 grains
Salts	85·6 „

On a diet consisting of meat 2·75 lbs. and fat ·55 lb., the following was the composition:

Amount	1·28 pints
Sp. gr.	1054
Urea	1,351 grains
Salts	189 „

Glycuronic acid exists only in traces, but after the administration of camphor or chloral it is obtained in well-marked quantities. It is a point of practical importance to avoid regarding urine which reduces salts of copper as necessarily containing sugar (see p. 301).

The Discharge of Urine.—The urine is constantly being secreted, and it either trickles down or is propelled down the ureters to the bladder by rhythmic muscular contractions. It is quite likely that both movements are employed depending upon the condition of bladder distension; whereas 'trickling' is suitable for an empty bladder, some muscular effort on the part of the ureters would be required when the bladder was full.

Either drop by drop or by 'spirts' the urine enters the bladder, which gradually advances in the pelvis, and rises up so as to touch the rectum. All reflux of urine into the ureters is prevented by the oblique manner in which the coats of the bladder are pierced, so that the greater the internal strain the tighter are the ureters closed. If circumstances prevent the evacuation of the bladder contents, the organ gradually advances to the brim of the pelvis, and then impinges on the abdominal cavity; in a state of extreme distension it may project for some distance into the cavity, the weight of the fluid having a tendency to cause the organ to incline towards the floor of the abdomen.

The entrance to the urethra is controlled by a circular layer of unstriped muscle, part of the bladder muscle, but outside this is a band of voluntary muscle which must be regarded as part of the urethra. Bladder pressure produces a desire to evacuate, an act which may be a purely reflex one, as in the case of the dog, with its spinal cord divided far forward, or, what is more common, as a voluntary act in obedience to the summons issued by the bladder wall.

Physiologists are not agreed as to how the act of micturition is carried out, but through the bladder wall impulses are transmitted to the cord, resulting in a contraction of the organ and a relaxation of the sphincters, though there is some difference of opinion as to this. At the moment the bladder wall begins to contract, it is assisted by the abdominal muscles and a fixed diaphragm, and the flow is never as powerful in the female as in the male, the final expulsion of the last drops from the urethra of the latter being given by the rhythmical contraction of the perineal muscles and *accelerator urinæ*.

The bladder receives a motor nerve supply through fibres coming off from the lumbar cord, which reach it by the mesenteric ganglion, and fibres coming off from the sacral cord which reach the bladder through the *nervi erigentes*. It is this latter group which causes an energetic contraction of the bladder. The sensory nerves run in the fibres from the lumbar cord.

During the act both the horse and mare stand with the hind-legs extended and apart, resting on the toes of both hind feet, thereby sinking the posterior part of the body; the male animal also often advances the fore-legs in order to avoid getting them splashed; in this position the penis is protruded, and the tail raised and quivering. The stream which flows from the two sexes is very different in size, depending on the relative diameters of the urethral canal. The mare after urinating spasmodically erects the clitoris, the use of which it is difficult to see; it may be due to the passage of a hot alkaline fluid over a remarkably sensitive surface. The horse can under ordinary circumstances only pass urine when standing still, though both sexes can defæcate while trotting; but in a condition of œstrum the mare can empty her bladder while cantering. In the ox the urine simply dribbles away, owing to the curves in the urethral canal, and is directed towards the ground by the tuft of hair found on the extremity of the sheath. The ox can pass his urine while walking. The cow arches her back to urinate, but instead of extending her hind-limbs as does the mare, she brings them under the body, at the same time raising her tail.

The upright position is essential to micturition; no horse of either sex can evacuate the bladder while lying down, a point of extreme importance in practice. Further, it will be remembered that in an over-distended bladder the fundus hangs into the abdominal cavity, and is thus brought on a lower level than the urethra, both of which contribute to the difficulty of emptying an over-distended organ. As a horse cannot micturate at work, it is obvious that opportunity for this should be regularly afforded, or much suffering results.

Pathological.

There is scarcely any organ of the horse's body so free from disease as the kidneys. The material in the pelvis which looks like pus is really the natural mucus of the urine, mixed with insoluble lime salts. We have never found sugar in the horse's urine; proteid is not uncommon, but only as the result of inflammatory affection of the lungs and pleura.

CHAPTER XI

NUTRITION

Wear and tear is continually taking place in the bodies of all animals, and as fast as destruction occurs repair must follow. We have previously studied the various channels in the body which supply the income and furnish an outlet for the expenditure, but this is only the beginning and the end of the process. To attempt to trace the exact changes which occur, say in the body of a pig, in producing 1 lb. of living material from 5 lbs. of barley-meal, is an impossibility. All we can do is to interpret the coarser or more obvious processes which take place, that of the conversion of dead into living tissues being quite beyond our knowledge.

Composition of the Body.—The animal body consists of proteids, fats, salts, water, and a very small proportion of carbohydrate. Every food must either contain these principles, or be capable of conversion into them within the animal body. The following table from Lawes and Gilbert shows the relative proportion of these various tissues in oxen, sheep, and pigs, in 'store' condition:

	Ox.	*Sheep.*	*Pig.*
Water	59·0	58·9	57·9
Proteids	18·3	16·0	15·0
Fat	17·5	21·3	24·2
Ash	5·2	3·8	2·9

The water is always in the largest and, excluding the carbohydrate, the salts in the smallest proportion. The amount of fat depends upon the condition; in fat animals it may, roughly speaking, be three times the amount given in the above table. The great bulk of the body is represented by the muscles, and these hold half the water and half the proteid found in the system. The following table shows the proportion of the chief body constituents of an adult horse weighing 1,100 lbs., and it may be compared with that of a cat:

	Horse.	*Cat.*
Muscles and tendons	45 per cent.	45 per cent.
Bones	12·4 „	14·7 „
Skin	6·02 „	12·0 „
Blood	5·90 „	6·0
Abdominal viscera	5·49 „	
Thoracic „	1·60 „	

According to Lawes and Gilbert the following are the relations of parts in the ox, sheep, and pig for every 100 lbs. of living weight:

	Ox.	*Sheep.*	*Pig.*
Heart, lungs, liver, blood and spleen	7·0	7·8	6·6
Internal loose fat	4·6	6·9	1·6
Stomach and contents	1·6	7·5	1·8
Intestines „ „	2·7	8·6	6·2
Other offal parts	18·0	15·0	1·0
Muscle, bone and surrounding fat	59·8	59·2	82·6

Income and Expenditure.—In order to arrive at a knowledge of the processes involved in nutrition, tables of the income and expenditure of the body have been drawn up.

The *Income* of the body consists of carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, salts and water; these are contained in the food, the oxygen being mainly supplied by the air taken in at the lungs.

The *Expenditure* consists of the same elements, which are got rid of by the lungs, urine, and skin.

The **nitrogen** is excreted almost wholly by the urine, excepting in the horse, where there is a loss by the skin. It is usual to regard the urine nitrogen as a measure of the proteid changes in the system, and this is got rid of mainly as urea, and in smaller proportion as uric and hippuric acids, and minor nitrogen compounds. The **hydrogen** is excreted as water by the lungs, skin, and urine. The

carbon is largely got rid of by the lungs and urine, and in the horse by the skin. The **salts** are excreted by the kidneys and skin, and in the form of secretions. The **sulphur** is lost through the kidneys, epithelium, hair, and horn.

It is hardly necessary to add that in calculating the true income of the body the fæces may be subtracted without leading to any great error, since they consist chiefly of food which has either escaped being digested or is not digestible. At the same time, they do contain a certain amount of material which represents products of tissue change which have been excreted from the blood into the alimentary canal (p. 208). When the income balances the expenditure the body is in equilibrium: if the expenditure exceeds the income the body loses weight, and if the income is in excess of the expenditure the animal gains weight.

Metabolism.—By this term is understood the changes occurring in living tissues. It is evident from what has been said that constant breaking down and building up is taking place in the body; every muscular contraction, every respiration, the beating of the heart, and the movements of the bowels, all mean wear and tear, and as rapidly as a part is destroyed it must be replaced. The process of construction is known as **anabolism**, and of destruction as **katabolism**; in a perfect state of health these should be in equilibrium. Both repair and destruction are dependent upon definite chemical changes occurring in the system, of some of which we have a fair knowledge, while others are wrapped in obscurity.

The metabolism of the tissues is apparently under the influence of the nervous system. We have previously studied a good example of this in dealing with the secretory nerves of the submaxillary gland, and it is probable, though our information on the point is very defective, that under the guiding influence of the nervous system the nutrition of the body is largely maintained. We constantly observe muscular wasting in some forms of lameness and injury in the horse, which is out of all proportion to the atrophy a part suffers by being simply thrown out of use, and it can only be explained by injury to the trophic nerves which regulate the nutrition of the part. Even a better example is the peculiar changes which sometimes follow direct injury to trophic nerves, as in plantar neurectomy of the horse; the sloughing of the entire foot, or gelatinous degeneration of the phalanx, is due to injury of the trophic nerves. Injuries to the fifth pair of nerves have been followed by sloughing of the cornea, and pneumonia has followed division of the vagi, in both cases being possibly due to the loss of trophic influence, though much may be said in support of the view that the effects observed may be due to failure of the mechanically protective arrangements of the parts affected, the failure resulting from section of the merely motor and sensory fibres which the respective nerves contain.

But disordered nutrition of a tissue may show itself without any obvious injury to trophic nerves, as for example in the phenomenon known as inflammation, or the well-known sympathy existing between the digestive system of the horse and the laminæ of the feet. Further evidence of nervous action is afforded in nutrition which is normal in character, such as the change of the coat with the season of the year. The influence of light on metabolism is also probably effected through the nervous system; it appears certain that a connection between visual sensations and the nutrition of the skin occurs in blind men and animals, and the popular belief that a blind horse carries a heavy coat in summer and a short one in winter may be something more than mere superstition. In making these statements we must guard against the error of considering that no growth, repair, or reproduction can take place excepting under the influence of the nervous system; the trophic influence exercised by nerves appears to be directed to maintaining in equilibrium the processes of building up and breaking down which are occurring in all tissues. Though the metabolism of the body is largely regulated by the nervous system, yet the process cannot be carried out without food. It is true that metabolism goes on during starvation, but even then food is being supplied, inasmuch as the animal is living on its own tissues.

The food must contain the elements required by the tissues, viz., water, proteid, fat (or carbohydrate) and salts; each of these must be in proper proportion, neither deficient nor in excess of the animal's requirements; each must be present, fat cannot be substituted for proteid, nothing can take the place of salts, and a water-free diet sustains life less long than does the entire absence of food as long as water is consumed. We have, therefore, to inquire why it is these substances are absolutely essential in every diet, and how they behave in the system.

Nitrogenous Food.—The history of **proteid** in the body may be conveniently taken up at the point where it was left when dealing with absorption, viz., in the bloodvessels. It will be remembered that as peptone the material passed from the bowel to the blood, yet no peptone can be detected in blood, showing that a regeneration has occurred, the peptone being converted back to proteid. We do not know whether the whole of the proteid in its downward course from complexity to simplicity becomes body-proteid, such as would be represented by the serum of blood, or whether a part only undergoes this change while the remaining portion is converted into leucine, tyrosine, arginine, etc., and is not built into proteid, but becomes urea.

The interest attached to knowing how the proteid of the food behaves in the body, arises from the remarkable fact that nearly the whole of the nitrogen in it can be recovered from the excretions; very little, and under some circumstances none, is stored up. So that the question arises as to whether the nitrogen of the excreta arises from preformed proteid tissue, or from the nitrogen last consumed, and if the latter whether it was from recently formed body proteid, or only material in the leucine or tyrosine condition? It is in an endeavour to answer these questions that the bulk of the work on metabolism has been carried out, and the results group themselves into two theories, Pflüger's and Voit's. Pflüger holds that the whole of the absorbed material must first be converted into proteid before any destruction of it can occur; in other words, that there is no short cut to urea excepting through the disintegration of the living cell. Voit contends that the proteid when absorbed is divided into two portions: one, the smaller, repairs wear and tear in the body and is spoken of as *tissue proteid;* the other, the larger portion, circulates with the blood and lymph and bathes the body cells, but does not form part of them. This is destroyed by the tissues with the liberation of heat and the formation of nitrogenous end-products, the chief of which is urea; this portion Voit describes as the *circulating proteid.* Voit's theory has been subjected to severe criticism, and the experiments on which it is based have been shown to be not entirely free from error, yet there is much in it which explains the observed facts of nitrogenous metabolism.

Nitrogenous Equilibrium.—If an animal in poor condition, or a young growing animal, be fed on an ordinary diet, it will be found that the whole of the nitrogen is not recoverable from the excreta, as described above, so that evidently some has been retained in the body and stored up; further, under the conditions of a liberal diet and active muscular work, the muscles grow and for this purpose they retain nitrogen. But speaking generally all the nitrogen consumed is practically recoverable from the excreta. If the nitrogen of the food be increased that of the excreta is increased; if it be reduced the nitrogen excreted becomes reduced, and this may be maintained through long periods of time.

It is certainly a very remarkable fact that the body should be able to work under ordinary circumstances equally well on a moderate as on a large supply of proteid. The influence of this may be still further tested by placing the animal on a diet *entirely proteid.* The effect of such a diet is to cause at once an increased elimination of nitrogen by the kidneys, so that more is actually being cast off from the body than enters by the mouth. If in order to meet this loss further proteid be given, a larger and still excessive excretion of nitrogen continues. Experiment, in fact, determines that it is not until three times the usual amount of proteid is given that the nitrogen entering by the mouth equals that excreted by the kidneys. When this condition is reached the animal is said to be in *nitrogenous equilibrium*. It is obvious that this is an artificial state and cannot possibly be maintained for long; further, it is impossible to bring it about unless the animal starts the experiment with some stored-up fat in the body.

The diet necessary for the production of nitrogenous equilibrium is seriously deficient in carbon, and the reason why the animal goes on consuming proteid and increasing its excretion of urea is in order to obtain the needful carbon; proteid contains 54 per cent. of carbon, while fat contains 76·5 per cent. It is quite possible on a large nitrogenous diet for the animal to continue to lose weight in consequence of the body carbon being drawn on; on the other hand, should it gain weight the material which is stored up is not proteid, for we have shown that all the nitrogen appears in the urine. The stored-up substance is carbohydrate and perhaps fat, though this latter point is not yet decided. Proteid in the body splits into a nitrogenous and non-nitrogenous moiety; it is from the latter that glycogen and perhaps fat are obtained, the former, of course, furnishing the urea.

In nitrogenous equilibrium there is carbon starvation, and if the explanation given above is correct, that the increased consumption of proteids is due to the urgent need for their carbon, then the addition of carbon to the diet will cause a reduction in the amount of proteid metabolised. And this is found to be the case. The addition of either starch or fat to the diet at once causes a reduction in the amount of proteid necessarily ingested in order to maintain the condition of nitrogenous equilibrium; this is known as the *proteid sparing* action of starch and fat, and is one of the few well-established facts in metabolism and the basis of rational dieting.

It has long been observed that many diets were excessively nitrogenous and therefore costly and wasteful; in exact experiments on men it has been shown they can be kept in health for months on a diet far poorer in proteid than what is generally accepted to be necessary. It is extravagance to give 2 pounds of proteid daily to a horse if 8 ounces will meet all necessities. It is at this point the physiologist comes into conflict with practical experience. Theory says the quantity of nitrogen required is nearly independent of muscular work; practice says the harder the machine is worked the more nitrogen must be given. Theory says proteids are not the source of muscular energy, as this is the function of non-nitrogenous food; practice replies that may be so, but we know from experience that, whether we are getting a horse fit for hard work or cattle and sheep ready for the butcher, the diets given must be strongly nitrogenous and limited only by the appetite. In this matter our personal experience places us on the side of practice and opposed to theories. Why the hard-worked horse needs more nitrogen we are not prepared to explain. The suggestion that the machine works more easily and smoothly on a liberal nitrogenous diet does not bring us any nearer to a solution of the problem, but the fact remains that whatever may be the energy obtainable from starch and fat this energy is in some unknown way directed by proteid. All nitrogen over and above that required for repair was considered a wasteful or '*luxus consumption*,' a condition to which we by no means subscribe. That a wasteful consumption of proteid occurs where horses are not fed in accordance with the work they are performing is undoubted; the excess of nitrogenous material throws an additional strain on the excreting channels, and it is certain that, clinically, we are able to recognize the effects of a highly nitrogenous diet in the liver disorders of tropical climates, and lymphangitis and azoturia of the temperate latitudes.

Doubtful and difficult of solution as many of the important points are in nitrogenous feeding, they are nothing in comparison with the problem of how the dead food-proteid is converted into the living body-proteid, and how the same kind of proteid can be utilized in building up material so different in structure as bone and brain, muscle and fat, liver and skin.

It is here convenient to summarize what we have learnt regarding nitrogenous food :

1. The body requires nitrogen ; no diet is complete without it, nor can life be permanently supported in its absence.

2. The body having obtained its nitrogen stores up the small amount required to replace wear and tear and excretes the whole of the remainder mainly in the form of urea.

3. The assumption that the proteids are the source of muscular energy is incorrect, this being the function of non-nitrogenous food, yet increased muscular efforts must be met by an increased nitrogenous ration, the assumption being that in some unknown way it directs the production of energy in the muscle machine, after which it is completely cast off.

4. Proteid is stored up in young growing animals and in those out of condition ; some is also stored up in working animals so long as their muscles are increasing in bulk. It is considered that proteid cannot, under ordinary circumstances, be stored unless there is accompanying muscular effort, and even then there is a limit to the growth of muscular tissue, just as there is to the skeleton to which it is attached.

All true proteids are equally capable of becoming part of the tissues when taken as food, but when *albuminoids*, such as gelatin, are consumed, they produce the same amount of urea as an assimilable proteid, but the animal loses flesh, viz., none of the material is stored up in the system ; when gelatin is mixed with proteid it exercises a sparing action upon the latter, and less of it is used up in the body.

Non-nitrogenous Food.—The whole of the carbo-hydrate matters found in food, viz., the starch, sugar, gum and cellulose, must, as we have seen, be first rendered soluble before they can enter the system. Further, they can only enter as some form of sugar, and are then stored up for future use as fat in certain depots, and as glycogen in the muscles and liver, while for present use they exist as glucose in the circulating blood.

The supply of carbo-hydrates is added to by the splitting up of proteids into a nitrogenous and non-nitrogenous portion (p. 320); whether the non-nitrogenous portion of proteid can form fat is uncertain, but it is undoubted that it forms glycogen.

Carbo-hydrates are readily oxidized as the molecule provides sufficient oxygen to oxidize all its hydrogen, and only needs to obtain from the tissues oxygen for the oxidation of the carbon. In this respect they are a great contrast to the fats, in which the proportion of oxygen to hydrogen in the molecule is not sufficient to oxidize all the hydrogen to water, so that fats have to obtain oxygen both for their hydrogen and carbon. In dealing at p. 96 with the question of the respiratory quotient it was explained that this fraction represented the relative amounts of carbonic acid produced and oxygen absorbed. The theoretical value of the respiratory quotient on a carbo-hydrate diet is 1, but with fats the volume of oxygen absorbed is greater than the volume of carbonic acid produced, and the respiratory quotient becomes ·707.

1 gramme (15½ grains) of carbo-hydrate requires ·832 litre (50·8 cubic inches) of oxygen, and produces ·832 litre (50·8 cubic inches) of CO_2.

1 gramme (15½ grains) of fat requires 2·8875 litres (176 cubic inches) of oxygen and produces 1·434 litres (87·5 cubic inches) of CO_2.

Great interest attaches to the carbo-hydrates in the feeding of herbivora, as so little fat exists naturally in vegetable food. We have learnt that the carbo-hydrates are one of the sources of muscular energy, and with horses they are the chief source. This material is 'fired off' by the muscles during contraction, and so markedly are carbo-hydrates the source of muscular work, that the whole store in the body may be used up under the influence of muscular work and starvation.

As the result of the oxidation of carbo-hydrates heat is generated, so that these substances supply not only energy but heat to the body. The seat of the necessary oxidation is in the tissues and not in the blood; the tissues produce enzymes which break up the sugar with the formation of carbonic acid and water; these enzymes are called into activity by the internal secretion of the pancreas. The amount of heat generated by the oxidation of sugar can easily be measured, 1 gramme (15½ grains) yielding 4,100 calories, or 4·0 large calories of heat.* Oxidations are constantly going on throughout the life of the animal; those occurring during rest are providing for the internal work and heat of the body, while during work, in addition to these, they furnish the muscular energy.

The influence of carbo-hydrate as a proteid sparer has already been mentioned; 10 per cent. less proteid is required with the food when carbo-hydrates are present in sufficient quantity. Experiment even shows that under the influence of a considerable quantity of carbo-hydrate, no more proteid is required by the system than is equivalent to the urea excreted during starvation. In spite of the immense value of carbo-hydrates in feeding, a diet of carbo-hydrate without proteid means starvation.

The Fats.—As previously noted there is very little fat in the diet of herbivora, in fact the amount is so small that in the fattening of animals fat is always specially added to the diet.

It might hence be natural to conclude that the fat in the body is derived from the fat in the food, but this does not cover the whole ground; great stores of fat may exist in animals receiving a trifling amount of fat in the diet: a cow, for instance, may produce more fat in her milk than she receives in her food, so that it is evident a something not fat is furnishing it. This something is the carbo-hydrate which when in excess of requirements is stored up as fat in the permanent fat reserve depots of the body, and subsequently doled out to the system as required. Perhaps also the non-nitrogenous portion of the proteid molecule may contribute to fat formation, though this point is not settled.

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* A *large* calorie is the amount of heat necessary to raise 1 kilo. (2·2 lbs.) water 1° C. (1·8° F.), and is conveniently named a kilocalorie.

The storing up of fat is a physiological process, though under certain circumstances it may constitute a pathological condition. By its oxidation, which is referred to more fully at p. 332, fat furnishes heat and energy, and in this respect is of higher value than an equal quantity of carbo-hydrate. One gramme (15½ grains) of fat yields 9·3 *large* calories on oxidation. How it is prepared for oxidation is unknown; the fat as it lies in masses in the body cannot be oxidized until it is brought back into the blood and carried to the tissues, and it is suggested that the fat-splitting ferment, *lipase*, decomposes the fats into fatty acids and glycerin, in much the same way that the same ferment splits the fat in the intestinal canal before absorption. Should this be the case the lipase regulates the supply of fat to the blood.

There are certain fat reserve depots natural to the animal, and on which under ordinary circumstances little or no drain occurs; such are found beneath the peritoneum, around the kidneys, in the mesh of the omenta, and surrounding the base of the heart. It is only under the influence of starvation that the fat in these places is drawn on. The chief means to induce the laying on of fat is a liberal diet and freedom from exercise and work. The farmer feeding for beef or mutton understands the value of keeping the animals as quiet as possible, and recognizes also that there are certain breeds which have a distinct predisposition to store up fat. He further learns how necessary it is to introduce animals gradually to a fattening diet until toleration is established, and he knows from practical experience that he will not succeed in fattening within a reasonable time unless to the diet of carbohydrate and fat he also adds proteids liberally. The measure of the diet is that of the animal's appetite; they can never eat enough to please the feeder, who cheerfully accepts the heavy initial outlay, as he knows the subsequent saving in time effected. The obesity aimed at with 'show' cattle, sheep, and pigs is a pathological condition repugnant to common sense, and the outcome of a barbarous fashion.

The consensus of opinion is in favour of castration as facilitating fattening, though this view has not stood the test of scientific enquiry. It is conceivable that if it has some such effect, it may easily be explained on the ground of greater freedom from excitement. It is quite certain that geldings have no greater disposition to accumulate fat than mares, and if castration favoured fattening there would be no need for that constant striving after fatness instead of 'fitness,' which is so characteristic of all who have charge of horses. There are, of course, some animals which have a tendency to store up fat and others which never do any credit to their 'keep,' but this is an individual peculiarity not explained by castration.

The fat of horses is soft and of sheep hard; that of cattle occupies a middle position. Each animal has fat of a certain melting-point to store up, and whether this be derived from oil, carbo-hydrate or food fat, makes very little if any difference. In the fattening of the herbivora it is considered that carbo-hydrates are better fat producers than food fat. The form in which the fats in food are stored up has been made the subject of many experiments: a dog fed on a hard fat converts it into canine fat which is soft; cattle fed on fluid fats, like linseed oil, convert them into hard body fats; still, experiments go to show that foreign fats used for feeding may, if given in sufficient amount, be recognized in the tissues. It is considered that green food, hay, and carbo-hydrates, produce a hard body fat, while grain feeding, such as oats, conduce to a soft fat. Fats, like carbo-hydrates, exert a sparing action on proteids, and for this reason a fat animal takes longer to starve to death than one which is less fat.

Inorganic Food. — The salts in the body perform important functions in connection with secretion and excretion; as Foster expresses it, they direct the metabolism of the body, though how they do so is unknown. To their presence is due the normal composition of the body fluids and tissues, for they regulate the water-flow from blood to tissues and *vice versa.* Proteids which are free from salts are quite altered in their essential characters, while the part taken by the salts of the body in blood-clotting, rhythmical contraction of the heart, irritability of muscle and nerve, milk-curdling, and growth is of supreme importance. The distribution of the salts throughout the structure is remarkably regular, sodium being found in the blood plasma, potassium and iron in the red cells, sulphur in hair and horn, potassium in sweat, sulphur in proteid, and lime in bones, etc. Animals fed on a diet which is as far as possible rendered free from salts soon die. When a deficiency in salts occurs, the body apparently for some time draws on its own store, and then certain nutritive changes follow. Cattle in South Africa suffer from inflammatory conditions of the skeleton (*osteo-malacia*) in consequence of deficiency of phosphate of lime, and the disease can be cured by its administration. Young animals may exhibit nutritive changes in the bones owing to a diet poor in calcium salts.

The chief salt used by herbivora is potassium, whilst sodium is used by carnivora. Both carnivora and herbivora obtain in their natural diet a sufficiency of these salts, though the general impression is, that the wild herbivora long for sodium. It is quite certain that under the conditions of domestication horses can be kept in perfect health without receiving any sodium chloride, other than that contained in the food, and the amount of this in vegetable substances is small. The iron required by the blood is probably furnished in some organic combination. It is evident that the daily quantity of salts required must depend upon the age of the animal, young growing animals requiring more than adults.

Storage of Tissue.—Every diet must contain the food principles we have been considering, viz. :

Proteid.
Fat or *carbohydrate*, or both.
Salts.

It is interesting to learn in what proportion these are stored up in animals being fattened, also the amount of food required for a definite increase in weight, and the rate at which that increase occurs. This is shown in the following table from the classical experiments of Lawes and Gilbert :

PROPORTION OF FOOD PRINCIPLES STORED UP FOR EVERY 100 LBS. INCREASE OF BODY WEIGHT.

	Proteid.	Fat.	Salts.	Amount of Dry Substance in Food required to produce 100 lbs. Increase in Weight.	Weekly Increase in Body Weight.
Oxen - -	9·0	58	1·6	1,109	1·0 %
Sheep - -	7·5	68	2·0	912	1·75 %
Pigs - -	7·0	66	0·8	420	6 to 6·5 %

The table shows that in all cases the chief increase in body weight is due to the deposition of fat. The ox lays on the most proteid, the sheep stores up the largest amount of salts, the pig puts on the most fat, and fattens, not only on the smallest amount of food, but in the shortest time.

Water.—The amount of water found in the tissues of animals is very constant, as may be seen from the table on p. 314, where the body water in different animals varies only from 57·9 per cent. to 59 per cent. The muscles of creatures as far removed as the pig and the snail, the ox and the lobster, contain 78 to 79 per cent., and other tissues are equally uniform.

Under the influence of rest and work varying quantities of water are lost, and in hot weather the loss is still further increased. It has been calculated that a man may lose water at the rate of 5 per cent. of his body weight on a hot day, and that muscular work in hot weather may increase the output of water as much as six times, but we are not aware of any exact experiment on this question on animals, though we know practically that the loss of water is considerable. Of the total water received in the food or consumed, the bulk passes away by the kidneys; during work a considerable amount is lost by the skin and lungs, and less in consequence passes by the kidneys.

The very constant proportion of water in the tissues shows that the consumption of excessive amounts of fluid does not lead to storage. Adjustments are readily effected and the excess of fluid in the blood is rapidly got rid of. All animals withstand a deficiency of water badly; the horse is probably the weakest in this direction, and shortage of water is far more immediately serious for any horse than shortage of rations. A thirsting animal dies when it has lost 10 per cent. of its body weight in water, though 50 per cent. of its proteid and the whole of its fat will disappear before death from starvation ensues. A man may avoid putting on weight by keeping himself short of fluid, and horses will rapidly lose condition by having their water supply limited. Without sufficient water intestinal digestion in herbivora cannot go on; the contents of the colon and cæcum of the horse must be kept fluid, and much of the water consumed is devoted to the purposes of digestion. Further, the blood must be kept fluid and concentration avoided; in the first instance the concentrated blood draws on the tissues for fluid, but later on this source dries up, and unless dilution of the blood be effected, death is only a matter of time, and with horses undergoing severe exertion, a very short time before complete collapse occurs.

Starvation.—When an animal is starved it lives on its own tissues; in the herbivora the urine becomes acid, hippuric is replaced by uric acid, and the secretion becomes transparent. The elimination of nitrogen by the starving animal at first falls rapidly, then gradually, and shortly reaches a fluctuating daily quantity. During starvation the carbonic acid excreted falls in amount, and the oxygen absorbed becomes reduced, though not in proportion to the fall of carbonic acid. If water be given life is considerably prolonged; Colin records a case where a horse receiving water lived thirty days without food. It is notorious that herbivora, though they lose less proteid during starvation than carnivora, do not withstand starvation so well; nor need we go so far as a starvation experiment to ascertain this fact. When men and horses are being hard worked, the loss in condition amongst the horses sets in early, and is extremely marked for some time before the men show any appreciable muscular waste.

Horses have been known to live without food or water for as long as threc and dogs for four weeks; but it is said that if horses have suffered 15 days' starvation, the administration of food after this time will not save them. Colin records an experiment where a horse weighing 892 lbs. died after 30 days' starvation, only being allowed 2½ pints of water per diem. The animal was nourished on its own tissues, the daily loss in weight being 5·9 lbs., which must be considered as exceptionally small. Dewar* records two remarkable instances of the length of time sheep will withstand starvation; in one instance eighteen sheep were buried in the snow for six weeks and only one died. In the second case seven sheep were buried for eight weeks and five days, and all were recovered alive and eventually did well.

In some very accurate experiments on a starving cat, it was shown that the principal loss occurred in the fat, 97 per cent. of which disappeared in 13 days. The following table shows the percentage of dry solid matter lost by the tissues:

Fat - - -	97 per cent.
Spleen - - -	63·1 „
Liver - - -	56·6 „
Muscles - - -	30·2 „
Blood - - -	17·6 „

The loss in the glandular organs was very heavy; next followed the muscles, and then the blood. The central nervous system suffered no loss; evidently its nutrition was kept up at the expense of other tissues of less importance. Old animals bear starvation much better than young growing ones, as their requirements are smaller.

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* *Veterinarian*, May, 1895.

Cause of Body Waste.—The work of the body may be described as internal and external. By *internal work* we refer to respiration, the action of the heart, movement of the bowels, animal heat, etc.; by *external work* is understood those movements of the muscles which transport the body. Every diet given to an animal must take these two factors into consideration; the *ration of subsistence* is the minimum diet necessary for the internal work of the body without incurring loss of weight, the animal, of course, doing no work; the *ration of labour* furnishes the actual muscular energy employed during work. The changes undergone by food in providing energy as heat and motion fall principally, if not exclusively, on the non-nitrogenous elements; this has been settled beyond all doubt. Considering that no animal can live on a nitrogen-free diet, and that the harder the work performed, the larger is the amount of nitrogen required, one would have thought, as Liebig did years ago, that the source of energy in food was the proteid substance. This is not so, therefore the urea is no measure whatever of the work performed, in fact is hardly affected by work, though it is largely affected by the amount of nitrogen received in the food.

During work the heart and respirations are quickened, the horse sweats, and a larger volume of air is warmed in the lungs; all this means a loss of heat to the body. In addition the muscles produce heat as the result of contraction, in fact every process seems to tell essentially on the non-nitrogenous elements of the body, which is the explanation why carbo-hydrates are so necessary in the diet of hard-worked horses.

The **Energy yielded by Food** has been ascertained by burning the substance in a calorimeter and measuring the amount of heat given off; in this way the potential energy of proteid, fat, and carbo-hydrate has been ascertained. Every 1 gramme (15·432 grains) of water in the calorimeter raised 1° C. (1·8° F.) is called a heat unit; by this method of investigation it has been found that

1 gramme of average proteid evolves, approximately, when oxidized, 5,770 heat units,* or 5·7 *large* calories.†

1 gramme of fat evolves, when oxidized, 9,300 heat units, or 9·3 *large* calories.

1 gramme of carbo-hydrate evolves, when oxidized, 4,100 heat units, or 4·1 *large* calories.

Proteids, unlike carbo-hydrates and fats, are not completely oxidized in the body, inasmuch as the nitrogen they contain reappears in the excreta in the form of urea. Now the complete oxidation of 1 gramme of urea yields 2,523 calories (or 2·5 kilo-calories), which must be subtracted from the value given above for the potential energy of proteids in order to ascertain the energy-value of proteids actually available by the body. Speaking approximately, 1 gramme of proteid gives rise to $\frac{1}{3}$ gramme of urea, hence the heat of combustion of proteids must be diminished by $\frac{1}{3}$ of 2,523 = 841 calories, before we apply the data to the body. This gives us a heat-value for average proteids of 4,929 calories or 4·9 kilo-calories, as based on purely physical determinations. As a matter of fact, all the nitrogen given as proteid does not reappear externally as urea, nor is it all excreted through the urine; some passes off in the fæces. Making allowance for this, it appears, from Rubner's valuable experiments on living animals, that the working value for an average proteid is about 4·1 kilo-calories.

The Amount of Food Required.—The minimum amount of food required by horses during idleness has been determined experimentally; the amount required for work cannot be fixed with precision owing to individual variations; what is sufficient for one is insufficient for another. Still,

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[*] One heat unit or small calorie is the quantity of heat necessary to raise 1 gramme of water 1° C. in temperature.

[†] For definition see footnote, p. 824.

diet tables for working horses have been constructed on the basis of the mean amount found by practical experience to be necessary.

Subsistence Diet.—This is the diet necessary for the internal work of the body, the weight of the animal remaining unchanged; it represents the minimum amount of food required by horses doing no work. Grandeau and Leclerc kept three horses for a period of from four to five months on a diet consisting of 17·6 lbs. (8 kilos.) of meadow hay. The animals led a life of idleness with the exception of receiving half an hour's walking exercise daily. The 17·6 lbs. of hay furnished as a mean 7·02 lbs. of dry digestible organic matter for every 1,000 lbs. of body weight; the 7·02 lbs. of organic matter contained ·538 lb. of digestible proteid. The subsistence diet for three horses for 24 hours was, therefore, as follows for every 1,000 lbs. of body weight:

Proteid - - - -	·538 lb.	·244 kilo.
Non-nitrogenous - - -	6·482 lbs.	2·946 kilos.
	7·020 lbs.	3·190 kilos.

This amount of hay (7·02 lbs.) contains the following elements:

Carbon - - -	3·563 lbs.		1·619 kilos.
Hydrogen - -	·385 lb.	(6·16 ozs.)	·175 kilo.
Oxygen - - -	2·986 lbs.		1·357 kilos.
Nitrogen - -	·086 lb.	(1·376 ozs.)	·039 kilo.

Assuming the correctness of Grandeau's observations, we may accept the above amounts of carbon, hydrogen, and nitrogen, as approximately representing a horse's requirements for 24 hours during idleness, the animal neither gaining nor losing weight. The ratio of nitrogen to carbon in the above diet is 1 : 41; the ratio of the proteids to the non-nitrogenous fats and carbo-hydrates is 1 : 12.

From a table furnished by Grandeau and Leclerc, it would appear that no matter what the nature of the diet may be, horses require between 7 lbs. and 8 lbs. of dry *digestible* organic matter daily for every 1,000 lbs. of body weight, in order to maintain the nutrition during idleness. The following is the table referred to:

Diet.	In the Ration.	Amount digested.	Amount for 1,000 lbs. of Body Weight.
Hay alone	14·08 lbs.	6·09 lbs.	7·02 lbs.
Maize and oat straw	11·57 ,,	8·33 ,,	8·22 ,,
Maize, oats, hay and straw	9·48 ,,	7·30 ,,	7·50 ,,
,, ,, ,, ,,	9·49 ,,	6·74 ,,	7·45 ,,
Oats alone (crushed)	8·59 ,,	6·41 ,,	7·02 ,,

In some German experiments made by Wolff on the subsistence ration, 8·3 lbs. of digestible dry organic material were found necessary to maintain the body weight, and from this the digestible fibre, 1·6 lbs., was deducted, as in the experience of Wolff the fibre digested by horses was of no value as sustenance either at work or rest. In our own experiments on the essential diet for horses, we found the body weight could be maintained on 12 lbs. hay.

The essential diet presupposes that the food possesses a sufficient proportion of digestible proteids. In one of Grandeau's experiments a horse received 33 lbs. of wheat-straw per diem which furnished 13 lbs. of digestible matter daily (nearly twice the amount actually required), but this diet only supplied ·157 lb. of digestible proteids, or less than one-third of the minimum, the result being the horse died from starvation. The essential diet for an ox weighing 1,000 lbs. is, according to the experiments of Wolff, ·5 lb. to ·6 lb. of proteid, and 7 lbs. to 8 lbs. of non-nitrogenous matter reckoned as starch; the ratio of nitrogenous to non-nitrogenous matters is as 1 : 14. According to the same authority sheep require a relatively larger essential diet, owing to the growth of the wool and its accompanying fat, viz., for 1,000 lbs. of live weight ·9 lb. of proteid and 10·8 lbs. of non-nitrogenous matter, the ratio being 1 : 12.

Working and Fattening Diet.—The diet for horses at work, and those for the fattening of cattle, sheep, and pigs, is a question of hygiene, and reference should be made to works on this subject.

Pathological.

Disorders of nutrition occur with every departure from the normal condition, though much more apparent in some disorders than others.

Fever.—The tissues are readily broken down in supplying fuel for the increased metabolism which is giving rise to the abnormally great production and loss of heat; both the fats and proteids suffer, and in some disorders it is remarkable how rapidly wasting occurs once it sets in. In acute lung cases this is very obvious—in a fortnight the patient may be a wreck. The increased nitrogenous metabolism which this indicates suggests an increased secretion of urea, but exact work in this direction is still much needed. During fever there is an increased excretion of CO_2, and absorption of oxygen; uric acid is formed by the herbivora, and the urine becomes acid.

Marked muscular waste may occur in the absence of fever; anything which causes a drain on the system, such as internal parasites, tuberculosis, internal growths, etc., may reduce the animal to little more than a skeleton. Starving, under-feeding or over-working of animals are obvious causes of metabolic change, while defective teeth are a frequent cause of the same.

Actual change in structure as the result of deficiency of a food element is mentioned on p. 327 as a cause of *osteomalacia*. **Osteoporosis** in the horse has also been considered as due to a deficiency of salts in the food, but the weight of evidence is against this view. An excess of salts in the bowel may be productive of considerable trouble. One form of intestinal calculus in the horse is due to the amount of ammonio-magnesium-phosphate existing in the bowel through feeding too largely on bran.

The food-supply may be deficient in proteids or carbo-hydra or both, or there may be an excess. Disorders from the latter cause are very evident in the horse. **Lymphangitis** and **hæmoglobinuria** are diseases of the horse intimately associated with over-feeding and idleness, and have no parallel in any other animal.

Broken wind is referred to at p. 120 as having its origin in errors in dieting and management, such as a bulky and innutritious food supply, or heavy work on a distended stomach. Apart from these, there may be other disorders of nutrition responsible, for even under good management the production of the disease is not entirely controlled.

CHAPTER XII

ANIMAL HEAT

Oxidations.—In dealing with internal respiration on p. 101 we learnt the fundamental fact that the oxidations of the body do not occur in the blood but in the tissues. By means of these oxidations heat is produced, and the substances which are oxidized, viz., proteid, fat, and carbohydrate, have already been studied in the chapters on digestion and nutrition. The manner in which oxidations are carried out in the tissues is not clearly understood, in fact, it is by no means decided how oxidations occur outside the body. The view that oxygen directly unites with the substances oxidized is no longer accepted, for it is known that oxidations do not occur in the absence of watery vapour. In spite of the fact that oxidations within and without the body are very similar, and in their results practically identical, the conditions under which each is effected are not the same, the great dividing line being the relatively low temperature at which oxidations in the body are effected. It is probable that oxidations in the tissues are effected under the influence of enzymes and not directly by the presence of oxygen in the tissues, for it can be shown that, provided sufficient oxygen be supplied, any further increase does not affect the rate of oxidation. We have had before us the evidence of ferments capable of splitting fat, of oxidizing sugar, of converting sugar into glycogen, glycogen into sugar, and of acting on proteids; all of these may be isolated from the body tissues, and are known as *intracellular* enzymes. Other evidence can also be adduced of the existence of tissue ferments, by the fact that living tissue removed from the body under suitable conditions will be found to digest itself. It is supposed that the enzymes of the body stimulate the oxygen to activity; such enzymes have been called **oxidases** and have been found both in plants and in the animal body. They have not, however, been found in connection with the oxidation of proteid, fat, or carbo-hydrate, though this may yet be demonstrated. An oxidase effects oxidation in the presence of oxygen, but enzymes, which only act in the presence of hydrogen peroxide, are called *peroxidases*. It is considered probable that the splitting up of food stuffs by ordinary hydrolytic ferments is the first stage in the process, and this is followed by the action of oxidases; to the latter is due the formation of carbon dioxide, water, etc., and the production of heat. The heat so formed is derived from the oxidation of food stuffs, as described in the chapter dealing with metabolism, the fats and carbo-hydrate probably yielding in the body the same amount of heat as they do in their combustion outside the body, while the nitrogenous moiety of the proteid is not fully oxidized inasmuch as urea and other waste products carry away with them at least one-third of the available energy of proteid (p. 332). How the heat so formed is distributed, maintained and lost, must now be considered.

The Body Temperature.—One important division of the animal kingdom is into warm-blooded and cold-blooded animals. A *poikilothermal* or cold-blooded animal is one in which the body temperature depends upon its external surroundings. When these are cold the bodies of such animals are cold, being about a degree or so higher than the medium in which they are living. Such a condition exists in reptiles, fish, etc. A *homoithermal* or warm-blooded animal is one in which the body temperature is independent within wide limits of the temperature of the medium in which they are living: whether this be high or low makes practically no difference. Between these two come a class partaking of the characters of each, *hibernating* animals which during the summer are homoithermal, and during the long winter sleep are poikilothermal.

The temperature of the body is not uniform, the interior is warmer than the exterior, and the blood in the interior veins is warmer than in the corresponding arteries. The blood in the veins leading from a gland in a state of activity has a higher temperature than the blood which enters the gland. In the animal body the hottest blood is found in the hepatic veins, while the blood in the posterior vena cava is hotter than that in the anterior. There is also a difference in the temperature of the blood in the right and left hearts; it is generally considered that the blood in the right heart is the warmest, though Colin found that in the horse the blood of the left side was the hottest. The brain has also a high temperature. The practical aspect of the question is that the interior of the body is hotter than the exterior. A surface temperature does not indicate the temperature of the body, which for clinical purposes should be taken in the rectum. With the air at freezing-point there may be as much as 5·4° Fahr. (3·0° C.) difference in temperature between the rectum and the thin skin of the breast in the horse, while at the same external temperature the limbs of this animal, which are naturally cold, in consequence of the underlying tissues having very little vascularity, may indicate 44° Fahr. (25·4° C.) difference between the pasterns and the rectum.

The Normal Temperature of Animals.—The wide differences which exist in the normal temperature of animals of the same class is remarkable. The following observations were made principally by Siedamgrotzky.

Horse: The temperature varies between 100·4° to 100·8° Fahr. (38·0° to 38·2° C.). Age has a slight influence:

From	2 to 5	years old	the temperature	is	-	100·6°
„	5 „ 10	„	„	„	-	100·4°
„	10 „ 15	„	„	„	-	100·8°
„	20	„	„	„		99·4 to 100·2°

Cattle: The normal temperature is from 101·8° to 102·0° Fahr. (38·7° to 38·8° C.). Wooldridge* places the mean temperature at 101·4° Fahr. (38·5° C.), and gives the variations at 100·4° Fahr. (38° C.) to 102·8° Fahr. (39·3° C.). Compared with the horse the daily variations are small. *Sheep:* In these animals the greatest variation in temperature occurs, viz., 101·3° to 105·8° Fahr. (38·4° to 41·0° C.); probably the majority of temperatures lie between 103·6° to 104·4° Fahr. (39·7° to 40·2° C.). The cause of the variation is unknown. *Swine:* The average temperature is 103·3° Fahr. (39·0° C.), varying from 100·9° to 105·4° Fahr. (38·2° to 40·7° C.). *Dog:* The dog is liable to important variations depending on the external temperature; according to Dieckerhoff it varies from 99·5° to 103·0° Fahr., (37·4° to 39·4° C.); other observers put it at 100·9°, 101·3,° and 101·7° Fahr. (38·2°, 38·4°, 38·7° C.).

Variations in Body Temperature.—A rise or fall in body temperature does not necessarily imply an increase or diminution in the production of heat. A rise of temperature might be caused by a contraction of the vessels of the skin, due to external cooling, sending a larger quantity of blood into the internal and therefore hotter parts of the body; or a fall of temperature may be due to the greater cooling which occurs when the vessels are dilated, as by an external rise of temperature. To demonstrate increased heat-production it is necessary to show that the metabolism is increased, that more oxygen is absorbed, and more carbonic acid produced. In all animals there is a daily variation in temperature, the lowest records being obtained in the early morning, 2 to 4 a.m., the highest in the evening, 6 to 8 p.m., after which the temperature falls during the night; these variations are due to metabolism, as will be shown presently. Muscular work and the oxidation of food are the chief sources of heat; during rest the metabolism sinks, the tide is low, while during activity it rises. The temperature of the young animal is higher than that of the adult, while the temperature of animals living in the open is lower than those under cover; in the case of the horse as much as 1° Fahr. difference in temperature has been registered under this condition. Other causes of variation in temperature will be considered presently. The thermometer does not tell us the amount of heat formed in the body, it only indicates the difference between the heat produced and the heat lost. These important points must now be studied.

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* 'The Temperature of Healthy Dairy Cattle.' See *Proceedings of the Royal Dublin Society*, vol. x., part iii., 1905.

Heat Production.—The chemical action occurring in tissues, other than the muscles, as oxidations and leading to the production of heat, have previously engaged our attention; the rest of these changes occur mainly in the skeletal muscles, in which four-fifths of the daily heat produced is generated, and in active glands such as the liver. The heat furnished by glandular activity is amply demonstrated in the liver, though certainly not in all secreting glands. The temperature of the blood in the hepatic veins is higher than in the portal, higher even than in the aorta. It was shown by Bernard that in the dog while the portal vein was registering 103·5° Fahr. (39·6° C.), the blood in the hepatic veins was 106·3° Fahr. (41·2° C.). Every muscular contraction leads to the formation of heat in the muscle substances. Experiments performed on the external masseter muscle of the horse showed that during contraction the thermometer registered 5·0° Fahr. (2·8° C.) higher than in the same muscle at rest. As the blood streams out of the muscle its temperature is higher than that in the corresponding artery, and in this way the whole mass of blood would have its temperature raised, were it not for mechanisms by which the heat is dissipated. But the excessive production of heat is not always met by a sufficiently rapid compensation by loss, and a high temperature may in consequence be produced as the result. This is a most important point in connection with working horses. In the case of man compensation is sufficiently rapid, and little or no rise of body temperature occurs as the result of work. In the horse it is otherwise; half an hour's trotting may raise the temperature from ·7° to 2·7° Fahr. above the normal, though the amount of rise is largely a question of 'condition'; temperatures of 104° to 105° Fahr. after hard work, especially in a hot sun, are not uncommon. With rest the temperature falls in the course of a few hours, the mechanism for getting rid of heat being able to cope with it. With animals unfit for work through want of condition the temperature may take longer to fall, or even remain above the normal sufficiently long to be designated febrile, and 'fatigue fever' is not unknown in man. Fever may be due either to excessive production of heat or defective dissipation. In the above case it is probable both factors are at work.

The act of feeding, which involves increased muscular activity, not only immediately, but subsequently in the muscles of the whole alimentary canal, raises the temperature of the body. In the dog the maximum is reached from six to nine hours after a meal, during which time from 20 to 25 per cent. more heat is produced. In the horse, according to Siedamgrotzky, the temperature as the result of feeding may rise ·4° to 1·4° Fahr. (·2° to ·8° C.), but, according to this observer, there is no similar rise in the ox, and Wooldridge found not more than ·3° F. in dairy cattle. That heat is formed during the masticatory processes we have already seen from the observations on the masseter muscles of the horse; but the mechanisms for regulating heat in the body are such that a rise of anything like 1·4° Fahr. as the result of feeding must be regarded as exceptional.

A liberal diet causes at once an increased production of heat. In the tropics, or with a high external temperature, even a moderate diet may greatly raise the amount of heat produced.

Influence of the Nervous System on Heat Production.—The muscles of the skeleton are not always actively contracting, yet heat is always being formed in them. The heat is produced as the result of muscle tonus, viz., the contracted condition of the muscles essential to posture. There is also in operation, even with the most trifling movement, an antagonism to muscular contraction. For example, the flexors of a limb cannot contract without the extensors being thrown into a condition to oppose the movement. This heat production in muscles is under the control of the nervous system. If an animal be poisoned with curare the motor end-plates in the muscles are paralysed, less heat is now being formed in them and the temperature sinks; in fact, the animal becomes for the time being practically cold-blooded, the body-temperature rising and falling with the surrounding temperature. The same condition may be produced by dividing the spinal cord behind the medulla. In chloroform narcosis heat production is greatly interfered with, and in prolonged operations this should be borne in mind and the loss of heat provided against. Shivering is a physiological process associated with the production of heat to compensate for a loss. The shivering which occurs with horses after being watered during winter is caused by the consumed water abstracting heat from the tissues in order that its temperature may be raised to that of the body. The 'freshness' of a horse on a winter's morning is the outcome of nervous impulses instinctively started with the object of generating more heat.

Apart from contraction it is believed that muscles are the seat of a quiescent heat production under the influence of the nervous system, and that chemical changes resulting in production of heat are generated as the result of nerve impulses. Experimental injury to the corpus striatum, the so-called 'heat puncture,' causes an increased production of heat which may last for some time, without apparently causing the animal any inconvenience. Heat centres have also been located in other portions of the brain, optic thalamus, septum lucidum, etc., and in the spinal cord. By some it is supposed that this extra heat production takes place in the liver, but the balance of opinion inclines to locating it in the muscles. No special set of thermogenic nerves has yet been proved to exist, and it is probable that the chemical changes presided over by a central heat centre are reflexly effected through the motor nerve fibres of the muscles. The bearing of this view on the increased production of heat in fevers and rapid muscular wasting in febrile conditions is obvious, and capable of explaining much which has hitherto been obscure.

Heat Loss.—Unless some conditions exist in the body for the regulation of the proper temperature, the heat resulting from metabolic activity would continue to raise it steadily until it accomplished the destruction of the animal, and that this is no mere figure of speech is evident from the fact that a horse produces sufficient heat during idleness to raise the body to boiling point in less than two days. In order to maintain the temperature at a constant point heat production and heat loss must balance. This balance may be struck either as the result of diminishing the production of heat or as the result of increasing the loss. The temperature of the body may rise either as the result of an actual increase in metabolism or through difficulties in getting rid of heat. The processes by which, within narrow limits, accurate and prompt adjustment is made is known as *heat regulation.*

If cold water be poured on a hot body the body is cooled; if the surface of a heated body be wetted and the water allowed to evaporate, the body is cooled. If a cold body be placed in contact with one which is hot, heat is lost. And processes somewhat similar to these are occurring in the animal body.

1. By *Radiation and Conduction* heat is lost to surrounding bodies, provided, of course, that they are at a temperature lower than the animal's. If the surrounding medium, air, wind, or such like, is hotter than the animal body, then heat is gained instead of being lost. The natural or artificial covering of animals, be it hair, wool, or clothing, checks the loss by radiation and conduction, as

in a dry condition they are bad conductors of heat. When wet, however, they are good conductors and a considerable amount of heat is lost from sweating or rain. Clothing acts by imprisoning a larger amount of warm air, the air so confined being a bad conductor.

2. By *Evaporation* from the skin the sweat is converted into vapour and heat is lost, the rapidity of the process depending on the humidity of the air and its rate of movement. The value of this evaporation as a source of heat loss in the horse is considerable, probably higher than the figure fixed for man, viz., 14·5 per cent. of the total, but no data are available. Evaporation is constantly occurring; when the amount of sweat is small it is evaporated as fast as it is produced, and this is referred to in the chapter on the skin as insensible perspiration. The sensible perspiration is that which is not evaporated as rapidly as it is produced, and is the source of a much greater loss of heat.

3. *Evaporation from the mouth and nostrils, warming of inspired air, and vapourizing of water from the lungs.* The former is a very valuable means of heat loss in those animals which do not sweat from the general surface of the skin; the moist nose and open mouth of the dog are good examples of the principle, and in a much smaller degree the bedewed muzzle of the ox. The warming of the inspired air and the vapourizing of water from the lungs are most important sources of heat loss in those animals which do not sweat. The panting respirations of the dog, and of cattle and sheep in 'show' condition, are simply a means of cooling the body by warming a larger volume of air, and so indeed are the hurried respirations of disease.

4. *By the urine and fæces* a loss of heat is incurred in warming the food and water to the temperature of the body. The amount of loss thus brought about must be relatively considerable, especially in winter, at which time of the year, as we have previously seen, the abstraction of heat is so great as to cause shivering; experiment shows that drinking a pailful of water at 50° F. may cause the body temperature of the horse to fall ·5° to ·9° F. A

diet of roots, containing as they do 80 per cent. water, is a heavy source of heat loss with cattle in winter, though both in the case of the water consumed and the succulent food ingested, no actual loss of heat occurs until these are excreted as urine and fæces.

The heat lost by conduction, radiation, and evaporation, is greater in small than in large animals, as small animals have a relatively greater surface exposed in proportion to their body weight. A dog of 66 lbs. weight will lose 79·5 per cent. of his body heat by radiation and conduction, and 20·5 per cent. by the evaporation of water, whereas a dog weighing 8 lbs. will lose 91 per cent. by radiation, etc., and 9 per cent. by water evaporation.

The skin as a source of loss of heat is largely controlled by the nervous system. Through the vaso-motor nerves the vessels of the skin are constricted or dilated; when the vessels are constricted the skin becomes pale (though this may not be seen owing to hair and pigment) and the blood is thrown upon the internal viscera, where it is additionally shielded from loss. In consequence the skin becomes cold and the loss of heat less, not merely as the result of the lessened radiation, but chiefly as the outcome of the diminished evaporation. When the vessels are dilated the skin becomes flushed and hot, the veins stand out with blood, and a large amount of heat is lost. This vaso-motor action is an automatic reflex act, as also is the nervous control over the sweat glands, by which more or less water is poured out on the surface of the body and heat lost by its evaporation, and is normally set in action by changes in the temperature of the surroundings.

The loss of heat is influenced by the thickness of the natural covering, its colour, etc. The loss of heat from a rabbit after shaving off the fur is one and a half times greater than before shaving. Sheep before shearing excrete less CO_2 and more H_2O than the same sheep after shearing. White rabbits lose 75 per cent. less of the heat lost by black or grey, for white not only absorbs less heat during the day but loses less heat at night. Grey horses are better suited to the tropics than any other colour, and black horses least of all. The black skin of the negro protects the deeper tissues from the sun's rays, from which it might be argued that black horses in theory should stand exposure to a tropical sun better than grey, but a grey horse has a black skin and the pigment prevents the rays from penetrating. Varnishing the skin causes a rapidly increased loss of heat, so that the animal dies from cold unless rolled up in cotton-wool (see p. 264).

Influence of Heat and Cold.---A moderate degree of cold applied to the external surface of the body increases the production of heat, due to increased oxidations. This results from reflex motor impulses discharged from the heat-regulating mechanism. At the same time the appetite is increased to meet the extra demand, and foods rich in fat are instinctively sought after by man. The same should be observed in the feeding of animals, and an increase allowed in the food to meet the extra oxidations, fat, if possible, forming part of it. The body will stand a considerable degree of cold, but a continuous fall in external temperature cannot be withstood; a point is reached where the rate of heat productions is below that of heat loss, and the animal dies from cold. Conversely the body is adjusted to withstand a moderately high external temperature; the heat of Arabia or India, which renders surrounding objects such as metal too hot to hold, is borne with impunity by the acclimatized horse; the heat-regulating mechanisms do not allow the external heat to be stored up, but a continuous rise in external temperature cannot be borne, and a point arrives when the heat kills, for the discharge of heat from the body ceases, it becomes stored up, and heat-stroke follows. A far higher temperature can be borne when the air is dry than when moist, as evaporation from the surface practically ceases in a moist atmosphere. When air has its humidity increased by 1 per cent. it raises the loss of radiation and conduction 32 per cent., while an increase by 25 per cent. in the humidity of the air is equal to an increase of 2° C. in the external air. At a temperature of 88° F. in an atmosphere saturated with vapour the regulating mechanism of man is exhausted, and a rise in body temperature occurs. Horses taken from cold to hot latitudes have to learn to compensate, and until they do so a marked rise in body temperature will occur as the result of standing in a hot sun, though doing no work. This passes away with acclimatization.

The loss of body heat among animals lying out at night is partly prevented by the fatty lining to the peritoneal cavity, which saves undue conduction of heat. Wet, combined with exposure, causes a more important loss of heat than mere cold. It has been shown from exact observations on man that a limb clothed in wet flannel lost 34·4 per cent. more heat than the same limb in dry flannel. Animals never look so wretchedly miserable as after a night of cold rain; under the conditions of active service a cold, wet night is certain to kill off the most debilitated.

A physiological resistance to cold can be obtained by training; the body learns to regulate its loss and production of heat, and this brings us to a consideration of the interesting practical point of the necessity of clothing for animals, especially for horses, in a state of domestication.

Some animals, such as the horse, ox, and sheep, are born fully developed and clothed; in a few minutes they pass from a temperature of certainly over 100° F. within the womb of the parent, to perhaps freezing-point on the bare ground. The power of regulating their temperature is fully established, and in a very short time this is assisted by muscular movements of the limbs, which are learnt very quickly; the gambols of young animals serve some other purpose than that of mere lightness of heart. If healthy, cold has no effect on these young creatures, provided the parent is able to supply sufficient nourishment. There are other animals, such as newly-born pups, kittens, rabbits, and certain birds, such as pigeons, which are born blind, helpless, and more or less naked; they cannot move, are unable to regulate their temperature, and if taken from the maternal warmth their body temperature steadily declines and they die from cold. In these the capacity for regulating body temperature does not develop for some little time after birth, and until locomotion becomes possible.

We have seen then that the young of the horse comes into the world prepared by its heat-regulating mechanisms to deal with the question of external temperature, and as time goes on this is supplemented by an extra growth of hair for winter use and a lighter covering for the summer. If no interference with the coat be practiced it is undoubted that no extra covering of any kind is required during the coldest weather, and even where the covering is of the lightest, as with the thoroughbred horse, it is sufficient for the purpose. The thoroughbred brood mares of this country, once they go to the stud, live in the open for the remainder of their lives and never wear a blanket. And practical experience tells us that this may be gradually imposed on all horses with impunity, even those which have been kept in hot stables. Coughs, colds, and inflammatory chest affections, usually attributed to cold, are practically unknown among horses living in the open, even during the coldest winter, and it is easy to show that these diseases are largely the result of the artificial conditions under which working horses have to live. Is it possible for working horses to be *clipped and yet wear no blankets?* This question is not only one of hygiene, but also of physiology. Practical experience tells us they may be clipped two or three times, even in the coldest winter, and *provided they are well fed* they take no harm. Colds are absolutely unknown, and the explanation of these facts is that the horse possesses in a high degree the power of regulating his temperature. The nervous mechanisms we have been studying are kept in active operation, diminishing loss or increasing production as the case may be. A somewhat similar mechanism must exist among the inhabitants of the Polar regions, who live during the winter in their huts, in a temperature which is never above freezing-point; adults, and even children, may expose parts of their bodies to the external air at a temperature at which mercury freezes. Such exposure to the European would certainly result in frost bite.

Clipping.—Siedamgrotzky observed the effect of clipping on the temperature of horses. He found that the temperature rose after clipping, and fell to normal about the fifth day. It was observed that clipped horses had during exercise a higher rectal temperature by 1·8° Fahr. than unclipped horses, and the return to normal temperature was more steady and regular with them than with unclipped. The rise in temperature after clipping may be due to vaso-motor action; less blood being in the skin, more will find its way to the viscera, viz., to parts of the body which have a naturally high temperature, the result being that the total mass of blood has its temperature raised. Another way of accounting for the rise in temperature after clipping is by supposing that an actual increase in the production of heat occurs. This may be due to stimulation of the skin influencing the heat-forming mechanism reflexly, either as the result of the mechanical stimulus, or of the increased cooling of the skin due to the removal of the coat. Colin clipped a horse on one side of the body and not on the other; the *subcutaneous* temperature in the stable was:

Clipped Side.	*Unclipped Side.*	*Difference.*
86·9°	95°	8·1°

The animal was now taken out into cold air at three degrees below freezing-point.

	Clipped Side.	*Unclipped Side.*	*Difference.*
In 30 minutes the subcutaneous temperature was - -	85·1°	94·1°	9·0°
2½ hours later - - -	79·9	95·0	15·1
1 hour " - - -	83·3	95·5	12·2
1 " " - - -	85·1	96·1	11·0

The cooling of the clipped side is very marked, the temperature continuing to fall for three hours, while the slight fall in the temperature of the unclipped side was restored to the normal in three hours.

Hibernation.—The effect of a fall in the temperature of the bodies of animals is to produce a depression of metabolism. This is well seen in some mammals, such as the dormouse, which sleep all the winter, during which time they live upon the store of fat laid up in the tissues during the summer. Owing to their depressed metabolism this store is found sufficient to keep them alive, though they wake up at the end of the winter mere skeletons. On waking up the body temperature rises by bounds to the normal, the animal then returning to the condition of an ordinary warm-blooded animal, until the recurrence of the next period of hibernation. As to the causes of this remarkable phenomenon we know but little. It is not confined to only one class of animals, since it occurs in mammals, amphibians, reptiles, etc. No purely anatomical differences suffice to explain why some animals hibernate and others do not. External cold is usually assumed offhand to be the initiating factor, assisted possibly by the lessened food supply at the approach of winter. But some other more recondite cause than either of these must exist, since marmots may sometimes hibernate in the summer, dormice will hibernate even if kept warm in the winter; cold will not necessarily cause an animal to hibernate except at the appropriate season, and *severe* cold may even arouse a hibernating animal from its state of torpor.

The **Amount of Heat produced** by animals depends upon the rate of their metabolism and the surface area of their bodies as a factor which determines loss of heat, and hence its production if the temperature of the body is to be kept easily constant. A large animal produces actually but not relatively more heat than a small one; a small animal, as has been previously stated, has a greater body surface relative to its weight than a large animal, and in this way its loss is more rapid. As heat production must balance heat loss, the small animal must lose more heat and therefore produce relatively more heat, than a large animal.

The heat produced is measured as heat-units or calories,* and the amount produced per hour for every 2·2 lbs. of body weight is given by Colin as follows:

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* See footnote, pp. 324, 332. The calorie referred to here in the text is the *large* calorie.

Horse - - - - -	2·1 calories.
Sheep - - - - -	2·6 ,,
Dog - - - - -	4·0 ,,

A horse loses, according to Colin, 20,684 large calories per diem, or sufficient heat to raise 4,550 gallons of water 1·8° Fahr., or to raise 44 gallons from freezing to boiling point. Wolff, quoted by Tereg, gives a table showing the heat lost per diem by cattle, horses, sheep, and pigs, for every 1,100 lbs. of body weight:

Horse at moderate work - -	24,500 calories (large).
,, hard work - - -	87,200 ,,
Ox resting, and on moderate diet -	18,600 ,,
Sheep, with fine wool - -	27,700 ,,
Pigs, fattening - - -	85,000 ,,

According to Despretz a dog loses 393 calories (large) in 24 hours, and a man 2,700 in the same time.

Post-mortem rises of temperature are frequently observed. The explanation afforded of a post-mortem rise in temperature is that metabolism is still occurring in the tissues, but since there is no circulation to carry the heat away the temperature of the part rises.

CHAPTER XIII

THE MUSCULAR SYSTEM

THE muscular system is the largest in the body, the skeletal muscles alone representing 45 per cent. of the body weight.

The regulation of the blood supply, the movements of the skeleton, the contraction of the heart, and the transport of the ingesta along the intestinal canal, are all examples of muscular movement, and further they are examples of different kinds of movement; the slowly moving intestinal canal is very different from the active skeletal muscles, and these with their long periods of activity and rest are greatly in contrast with the rhythmical movements of the heart.

Structure of Muscle.—There are three varieties of muscle in the body:

1. Voluntary, skeletal, striped, or red muscle.
2. Involuntary, pale, or unstriped muscle.
3. Heart muscle.

The *voluntary muscles* are generally in large masses known as flesh, and their function is to move the skeleton. The muscle mass consists of bundles, the bundles are composed of smaller bundles, the smaller bundles are made up of fibres. The fibre of a muscle does not run the length of the bundle; on the other hand a primitive fibre is only about 1 inch in length, and of microscopic thickness, viz., $\frac{1}{500}$ of an inch as an average. The fibre is developed from a single cell, and surrounded by a membrane, the *sarcolemma*. The contents of the fibre are semi-fluid and composed of fibrils, viz., minute thread-like masses, each of which is found to be alternately striped with a dark and light band. It is the striping which gives to muscle its characteristic microscopic appearance of striation. Histologists are not agreed as to the detailed structure of the fibrils, but Schäfer, whose views are accepted by most physiologists, regards the fibrils, or *sarcostyles* as he terms them, as divided into a series of masses placed end to end; each mass is known as a *sarcomere*, and possesses a dark centre and clear ends. The dark and light stripes which result from this arrangement are composed of different substances, at least they possess different physical properties. During contraction the fluid material in the clear ends flows into the dark centre by means of certain pores. Between the fibrils is a coarse network of material known as the *sarcoplasm*. It is generally believed that the fibril constitutes the contractile portion of the fibre, the sarcoplasm being of a nutritive nature.

The *nerve* supply to muscle is both motor and sensory: through the *sensory nerves* the brain is made acquainted with the position of the body and the condition of muscular tension. This involves the existence of a special *muscle sense* which plays such an important part in locomotion. In the muscles this sense is represented by special bodies generally found near tendons, called *neuro-muscular spindles*; these are from $\frac{1}{8}$ to $\frac{1}{3}$ of an inch in length, and $\frac{1}{125}$ of an inch in width; each spindle is of muscle surrounded by a sheath, and has a sensory nerve entering it at one end. Nervous structures, known as the *tendon organs of Golgi*, also exist in the tendons at their junction with the muscle fibres; they consist of spindle-like bodies connected with one or more fine medullated nerve-fibres. These nerves are in communication with certain areas in the cortex of the brain which are devoted to the 'muscle sense' (see 'Senses,' Section 4). The ordinary degree of sensibility in muscle is not very great unless the part be cramped or inflamed, though pain is caused when they are cut into. By means of the *motor nerves* the muscle is supplied with the impulses which bring about contraction, division of the motor nerves, or interference with their function, causing paralysis of the muscle or muscles supplied by them. Each motor nerve enters the primitive fibre about its centre, and terminates in a special organ known as an *end plate*. By means of *curari* this end plate may be paralyzed, in which case stimulation of the nerve leads to no muscular response in consequence of the block, though the muscle itself is still irritable and readily responds to direct stimulation.

Masses of material built up on the lines described above are intended for the transport of the body, for which purpose they are united to the skeleton either by tendons or by the direct insertion of their own fibres. In the muscles of the limbs the tendon attachment is the most usual, wherever in fact the parts are exposed to great strain. There are certain muscles in the machine where the strain on them is so considerable that tendinous material is intimately mixed up with the muscular tissue; this is well seen in the masseters, the muscles of the back, fore-arm, and thigh. In the horse provision is also made for the muscles of the limbs being rested without necessitating the animal's assuming a recumbent position, viz., by the check ligaments in the leg; by means of these an animal can sleep standing, and may remain standing for some weeks without suffering. During progression the entire strain of the body comes on the feet and the muscles of the limbs, and in such paces as galloping the muscular strain is enormous; for example, during the canter and gallop a weight equivalent to that of the whole body is imposed on a foreleg. But this is a question to be dealt with in the chapter on Locomotion.

Muscle Antagonism.—Every muscle or group of muscles possesses an antagonist, and though the antagonist may be equal in size this is not always the case, as for example the great difference between the bulk of the muscles which close the jaw as compared with the trifling size of those which open it. The grouping, in co-ordination of action, of voluntary muscles is a question to be considered later, in the chapter on the Senses. The interest which is here attached to antagonistic muscles is connected with the fact that it is this antagonism which keeps the muscles of the body slightly on the stretch, so that if one be cut across it gapes in consequence. This elastic tension ensures that no time is lost in a muscle coming into action, as there is no slack to take up; the muscle stands as it were at full cock.

Involuntary or pale muscle is not found in masses as is the red, but in thin sheets, which in places such as the bloodvessels are only of microscopic thickness. Pale muscle is employed throughout the whole length of the digestive canal from the stomach to the rectum; it is also found in the bladder, uterus, spleen, and bloodvessels. In none of these places is the sharp, short, active contraction of skeletal muscle required; slow, steady, deliberate movements are essential in the digestive canal; slow, steady, expulsive movements are necessary in the bladder and uterus, and even in the bloodvessels, where, as we have seen, the muscular tissue acts the part of a tap: it is sufficient if the tap be turned on or turned off slowly and steadily. When we come to study muscular contraction we shall see how rapidly the wave passes along a voluntary and how slowly along an involuntary muscle.

In structure pale muscle consists of nucleated spindle-shaped cells, dove-tailed, and held together by a cement substance; it is through the medium of this cement substance that the wave of excitation passes from cell to cell, thus forming a great contrast to red muscle, where, as we shall see, the whole contracts, not by the spread of the stimulus from one fibre to another, but as the result of all the fibres being stimulated simultaneously. There are nerves and ganglion-cells in abundance in pale muscle; the nerves, which are chiefly non-medullated, form a fine plexus, with the ganglion-cells placed at the junctions of the plexus. It is probably due to these that involuntary muscle continues to contract when all connections with the

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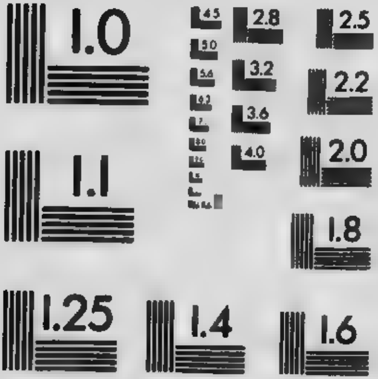

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centre are destroyed, though some physiologists see reason for thinking that the contraction of pale muscle may be carried out just like that of heart-muscle, viz., as a self-acting mechanism, independent of any nervous connections.

The nerve supply of involuntary muscle is peculiar and presents a great contrast to red muscle; whereas the latter only receives one variety of motor supply, pale muscle receives two, viz., one set of fibres which *stimulates* contraction, and another which *inhibits* it. Both sources are derived from the sympathetic system, which again is in great contrast to the arrangement of the nerve supply to red muscle.

Heart muscle is in structure both red and striated, nevertheless it is involuntary; the fibres are characterized by being formed of branched, nucleated, quadrilateral cells, while the sarcolemma is absent. As we have already seen, the contraction of the heart is primarily dependent on the properties of its muscle-substance, though the automatism is carefully directed by nervous mechanisms.

Muscular Contraction.—This apparently simple act is extremely complex, and will require to be dealt with in some little detail.

Muscles are tissues possessed of **irritability** and **contractility**, viz., they possess the power of responding by a movement to the application of a stimulus. The normal stimulus is effected through the motor nerves under the control of the brain or spinal cord, but of the nature of the stimulus we are ignorant. A coarse reproduction of it can be effected by pinching, pricking, chemical, thermal, or electrical stimuli, applied to either the nerve or the muscle itself, and to all these the three varieties of muscle are responsive. When a muscle contracts, in addition to becoming shorter and thicker, it also undergoes changes in its extensibility, elasticity, and temperature; there are also alterations in its electrical condition and chemical composition, and these can all be studied by employing a muscle of the frog, which retains its irritability for a long time after removal from the body. Such a muscle suitably prepared is known as a *muscle-nerve preparation*, and with certain modifications what is found to occur in this as the result of contraction, occurs also essentially in the living mammalian muscle.

The muscle most usually and conveniently employed for investigating the phenomena of muscular contraction is the *gastrocnemius* of a frog, dissected out in such a way as to leave its upper tendon connected with a piece of the femur and its lower tendon, the *tendo Achillis*, intact though free.

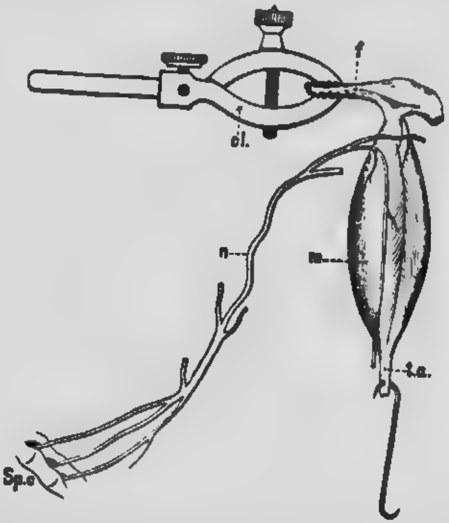

FIG. 75.—A MUSCLE-NERVE PREPARATION (FOSTER).

m, the *gastrocnemius* muscle of a frog; *n*, the *sciatic* nerve dissected out back to *Sp c*, the end of the spinal canal; *f*, femur; *ci*, clamp; *t a*, tendo Achillis with S-hook attached.

At the same time care is taken not to sever the connection of the muscle with its motor nerve, the *sciatic*, which is dissected out for some considerable distance back towards its point of exit from the spinal canal, the central end being, if desired, left connected to a portion of the spinal cord enclosed in a piece of the lower end of the spinal column. The muscle is then suspended by fixing the remains of the femur in a clamp; a small S-hook is then attached to the tendo Achillis. This muscle-nerve preparation and its arrangement as above described is shown in Fig. 75.

For purposes of experiment the clamp is fixed inside a small chamber with glass sides to prevent the drying of the muscle and nerve; this is effected by placing a few pieces of wet filter-paper inside the chamber. The sciatic nerve is laid over a pair of electrodes connected by wires to binding-screws outside the chamber; by this means any desired electrical stimulus may be applied to the nerve. A thread attached to the hook in the tendo Achillis passes through a hole in the floor of the moist chamber, and is connected with a horizontal lever free to move in a vertical plane, a small weight being hung under the lever to give the muscle the 'load' necessary for its efficient contraction. The free end of the lever is then brought to bear against the vertical surface of some recording apparatus, usually a cylindrical drum, covered with smoked paper, made to rotate by clockwork about a vertical axis.

The most conveniently controllable stimulus is that obtained as single induction currents or the interrupted current of an induction coil. These have the advantage of being extremely efficient as stimuli and of giving rise in the nerve to impulses which we may regard as the nearest artificial approach to the impulses which in the body are discharged along the nerves by the cells of the central nervous system. The complete arrangement of all the apparatus is clearly shown in Fig. 76.

An inspection of Fig. 76 shows at once that if the drum of the recording instrument alone rotates, the end of the lever connected to the muscle must trace out a horizontal line on the smoked surface. If the drum is stationary and the muscle is made to contract, the lever will trace a vertical line. If now the muscle is made to contract while the drum is rotating these two lines are compounded into a curve whose ordinates at each point of the curve and whose general shape give us exact information as to the details of the contraction from start to finish. Such a curve is called a 'muscle-curve' and is typically shown in Fig. 77.

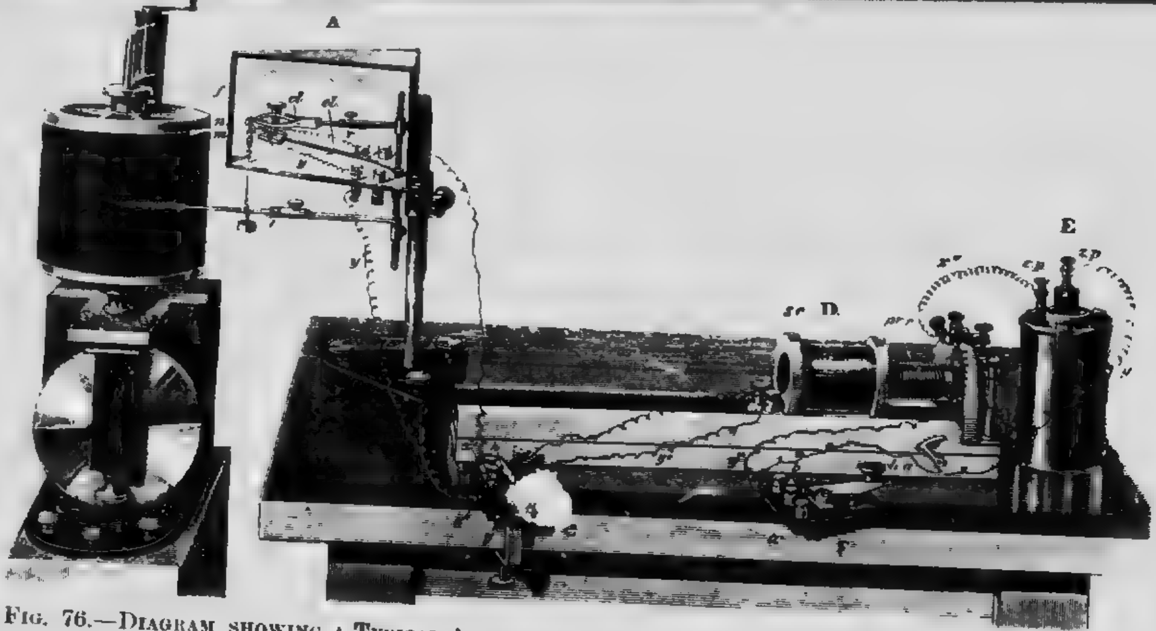

FIG. 76.—DIAGRAM SHOWING A TYPICAL ARRANGEMENT OF APPARATUS AND INSTRUMENTS FOR EXPERIMENTS WITH A MUSCLE-NERVE PREPARATION (FOSTER).

A, The moist chamber; *m*, muscle; *n*, nerve; *f*, femur; *cl*, clamp. The nerve is shown laid over the end of the electrode-holder *el*, connected by the wires *x y* to the outside of the chamber; *l*, the lever with which the muscle is connected by a thread and S-hooks. B, Rotating drum, carrying the smoked paper on which the lever makes its tracing. C, a key for controlling the connection of the electrodes in the moist chamber with the secondary circuit *s c* of the induction-coil D. F, a key for making or breaking the connection of the battery-cell E with *pr c*, the primary circuit of the induction-coil D.

At the moment of contraction the muscle becomes shorter and thicker, but there is no change of volume.

A muscle curve consists of three parts: (1) A period following stimulation during which no contraction occurs; it is known as the *latent period*, and during this time the muscle is preparing itself for work; (2) a period of *contraction* or shortening; (3) a period of *relaxation*. Some physiologists consider that a portion at least of the latent period may be due to instrumental defects.

The length of time involved in the various phases of a contraction may be measured by bringing a time-recorder, vibrating fractions of a second, to bear on the smoked surface of the revolving drum; the sinuous line in Fig. 77 below the muscle curve is produced in this way. Though the nerve was stimulated at the point marked 1 on the tracing, it was not until 2 was reached that the muscle responded, the time value for the latent period being $\frac{1}{100}$ of a second. The entire contraction from the instant of stimulation to the end of relaxation occupies about $\frac{1}{10}$ of a second. The time occupied in a contraction is influenced by the temperature of the muscle, and whether it be fresh or fatigued. The degree to which a muscle contracts is influenced by the weight it has to lift, the strength of the stimulus employed, and its state as to fatigue; the latter prolongs the latent period and renders the contractions slower and smaller.

FIG. 77.—THE CURVE FROM A SINGLE CONTRACTION OF THE GASTROCNEMIUS MUSCLE OF THE FROG (WALLER).

From 1 to 2 is the latent period; from 2 to 3 the period of shortening; from 3 to 4 the period of relaxation. The sinuous line below the curve indicates periods of $\frac{1}{100}$ of a second.

Muscle Wave.—When the impulse enters a muscle at the middle of each fibre, the part nearest the end plate contracts first, and the impulse spreads each way to the end of the fibre, but this process is so rapid, the fibre only being about 1 inch in length, that for all practical purposes the whole muscle contracts at one and the same time. If, however, the nerve-endings in a muscle be paralyzed by curare, the part becomes at once practically nerveless, and if now *one end* of the muscle be stimulated, a wave of contraction passes along it to the other at a rate of about 10 or 12 feet a second in the curarized muscle of the cold-blooded frog. In the muscles of warm-blooded man, where the metabolic processes are more active than in the frog, the rate of propagation is greater, and may be taken as 30 to 40 feet per second. The time which the wave takes to pass any *one* point of the muscle is extremely short, $\frac{1}{10}$ of a second, and if (in frog's muscle) we take its velocity as at least 10 feet per second, a simple calculation shows that the *length* of the wave is about 1 foot. This is a fact of great interest in connection with the efficiency of a muscle as a machine. It ensures that each single fibre, whose length, as we have said, is only 1 inch, of which the skeletal muscles are composed, and hence the whole muscle itself, is in a state of complete contraction, from end to end at the same moment during each contraction.

Summation.—If instead of passing a single stimulus into a muscle-nerve preparation, two are sent in, so arranged that the second follows the first before the muscle has time to relax from the first contraction, the contraction due to the second stimulus is superposed on the first, and the effect obtained is a stronger total contraction. If a third stimulus be sent in before relaxation occurs from the second, the lever of the muscle preparation will describe a curve still higher than the preceding, and so on, until a maximum is reached when it can go no higher. Such a piling up of contraction on contraction is known as *summation of contractions* (Fig. 78). It will be remembered that one characteristic of heart muscle is the absence of summation; the fibres of the heart yield their best possible contraction to a single stimulus, be it weak or strong, single or multiple.

Tetanus.—If an induction current be applied to a muscle or its nerve, a rapid succession of stimuli is thus introduced, and there is no time for complete relaxation to occur between each successive stimulus. This may be seen in the lower curve of Fig. 79, in which ten stimuli per second were passed into the muscle, and partial relaxation only will be observed to have occurred between each of them. In the middle curve twenty stimuli per second were used, and the amount of relaxation is represented by a slightly wavy line; in the upper curve thirty stimuli per second were employed, and the curve shows no relaxation; the muscle is in the condition of *tetanus*, and tetanus, therefore, consists of the summation of a series of short contractions with an insufficient interval for intervening relaxation.*

FIG. 78.—SUPERPOSITION OF CONTRACTIONS (STEWART).

1 is the curve of contraction due to the first stimulation; 2 is the curve of the second contraction, superadded to 1 by applying the second stimulus at the moment when the first contraction had nearly reached its maximum.

All the ordinary voluntary muscular contractions of the body have usually been regarded as tetanic in nature, viz., as a series resulting from a succession of impulses passed into the muscle so rapidly that there is no interval for relaxation. Other investigations have supported the view that in all probability a voluntary contraction is a prolonged single contraction, caused by one long constant stimulus. On the other hand, it has been urged, on the basis of experiments made by stimulating the motor areas of the cerebral cortex with stimuli of varying frequency, that a motor cell cannot discharge a single impulse, the normal rate in man under the influence of the will being ten per second. The question is, therefore, evidently not finally settled.

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* The tetanus of the physiologist must not be confused with the tetanus of the pathologist; the latter is a bacterial affection producing a poison which causes spasm of many of the voluntary muscles of the body, especially the limbs and jaw.

Elasticity and Extensibility.—Elasticity is the property a body possesses of returning to its shape after stretching, and this is very perfectly shown in living muscle; extensibility is the power a material possesses of stretching, and the amount of extensibility is tested by loading it with weights. If a steel spring or a piece of elastic be thus tested, it is found that the stretching is proportional to the weight employed, but if muscle be weighted it is found that the greatest degree of extension occurs at the beginning, and as the load is increased the extensibility becomes less. A contracted muscle is more extensible than one which is uncontracted, a protective mechanism intended to prevent

FIG. 79.—SUMMATION CURVES OF MUSCLE CONTRACTION (WALLER).

The lower curve is one obtained by stimulating the muscle ten times every second; the intervals of relaxation are clearly seen, though there is a slight summation shown by the slanting rise of the tracing. In the middle curve the shocks were twenty per second, and the relaxation is only of a very partial kind. The upper curve is that of tetanus.

rupture of the fibres during powerful muscular effort, and this is capable of ready proof clinically. A ruptured muscle is incomparably less frequent than a ruptured tendon.

In the body the muscles, as we pointed out previously, are always in a condition of *elastic tension*, viz., they are not slack, flabby masses, but slightly on the stretch, as may be demonstrated by the gaping which occurs when they are divided.

The use of this elastic tension is to stimulate the changes which lead to a contraction, also to ensure a rapid contraction without the necessity of taking in any 'slack,' and further it is essential to the proper action of the antagonistic muscles, which are thus enabled to work against an elastic resistance, and so cause a smoothness of motion otherwise unobtainable. The antagonistic action of muscles may be well seen in a rupture of the flexor metatarsi of the horse; the unbalanced action of the gastrocnemius jerks the leg behind the body, and throws the skin over the cap of the hock into folds, while the Achilles tendon is kinked and bent through slackness. The elastic tension of muscle is not only a valuable stimulus to contraction in all varieties of muscle, but is also of the greatest value in diminishing shock and strain; nowhere is this better seen than in the heart and bloodvessels.

Muscular *tone* is the name given to that condition of continuous slight contraction present in all the skeletal muscles, and leads to the elastic tension to which we have already referred. It is due to the continuous discharge of impulses, originated reflexly, by the central nervous system; if the nerves concerned in the production and discharge of these impulses be divided the tone is lost, and nutritive disturbances follow. Tone is also influenced by the quality of the blood-supply to the muscle and the efficient drainage of the part.

Work of Muscle.—If a muscle preparation be loaded with different weights, and the height to which these are lifted observed, it is found that up to a certain maximum the load absolutely increases the amount of work done by the muscles. This is considered to be due to the *tension* exercised on the fibres, as just explained. By gradually increasing the weight the muscle preparation becomes overloaded, and the muscle may now even elongate. These facts have been shown to be as true for mammalian as for frog's muscle, excepting that human muscle contains twice as much energy for the same volume.

If the weight of the load and the height to which it is lifted be known, the work done by a muscle is readily calculable. Work equals the load lifted multiplied by the height through which it is raised, and may be expressed as pounds or tons lifted 1 foot or grammes or kilogrammes lifted 1 metre.*

In connection with the work done by muscle it is interesting to institute a comparison between the work yielded by the animal body and that by a well-constructed machine. The best triple-expansion engine may yield as work some 10 to 15 per cent. of the available energy in the fuel, the balance is lost as heat; in other words, the 'efficiency'—that is, the fraction of the heat it receives which it converts into work—of a good engine is $\frac{1}{10}$ to $\frac{1}{7}$. In the animal body various statements have been made as to the proportion of work done to the available energy. Chauveau working with the lip-muscle of the horse placed the work at 12 per cent. to 15 per cent. of the energy liberated, the difference being accounted for as heat. If this were the case the muscle machine would seem to be very little more economical than the steam-engine. Now, Fick showed, some thirty years ago, that the efficiency of an *excised* muscle of the cold-blooded frog may be as much as $\frac{1}{4}$ or even $\frac{1}{3}$, and we may not unreasonably expect that mammalian muscle, in the body with its circulation intact, would be still more efficient. And this is borne out by Zuntz's experiments on the dog. He calculated that one-third of the energy liberated appeared as work, while by experiments on men it was found that the proportion was 25 per cent. as external work for the muscles of the arms (turning a wheel), and 35 to 40 per cent. for the legs (in mountaineering), from which it would appear that the muscles of locomotion are superior as work producers. If this be so it gives the animal body an 'efficiency' of from $\frac{1}{5}$ to nearly $\frac{1}{2}$, which far surpasses that of the best heat-engine.

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* A 'horse-power,' the unit used in engineering, equals 33,000 foot-pounds of work *per minute*.

Interesting as the comparison may be, a word of caution is necessary. It is true that an engine and a muscle each take in energy and utilize a part of it to do external work, but they work in different ways and along different lines to produce the same results. Thus the steam-engine receives its energy as heat, originated by the combustion of fuel in the boiler-furnace, converts a varying fraction of this into work and discharges the remainder, degraded in temperature but otherwise unaltered. A muscle, on the other hand, receives its energy in the form of the food it takes from the blood. This it metabolizes by chemical processes which are ultimately oxidational, converting the potential energy of the food partly into work and, unlike the engine, partly into heat (see p. 340), and giving off degraded products of its metabolism, of which one is the same as that from the furnace of an engine, viz., carbon dioxide. These few remarks must suffice to emphasize the fact that a muscle is a *chemical-engine* and not a heat-engine. As Fick was careful to point out, if one tries to explain the working of a muscle on the thermodynamic principles which govern the working of a heat-engine, one is landed in the absurd result that a muscle only converts into work $\frac{1}{100}$ part of the potential energy it receives, the remaining $\frac{99}{100}$ necessarily being converted into heat, and we have seen that the efficiency of a muscle may be $\frac{1}{3}$. In the case of insects, with their astounding locomotive activities, if the efficiency of their muscles could be determined it would probably be found to exceed that of mammalian muscle.

Muscle Currents.—Great controversy has taken place as to whether currents of electricity exist naturally in uninjured muscle. It was found, for instance, that a piece of muscle isolated from the body, and placed in connection with a galvanometer, may be made to demonstrate the presence of electric currents which behave in a perfectly regular manner, viz., under certain conditions they are always weaker, and under others stronger, in passing from one definite point on the muscle to another. These are the so-called natural *muscle currents*, or *currents of rest*; they are found to pass in a certain direction, viz., from the natural surface of the muscle to the cut extremity (Fig. 80). It is now distinctly known that the current obtained, as just described, is one caused by the *injury* inflicted on the muscle in its course of preparation for the experiment, the injured (end) point of the muscle being always negative to the less injured (equatorial) points.

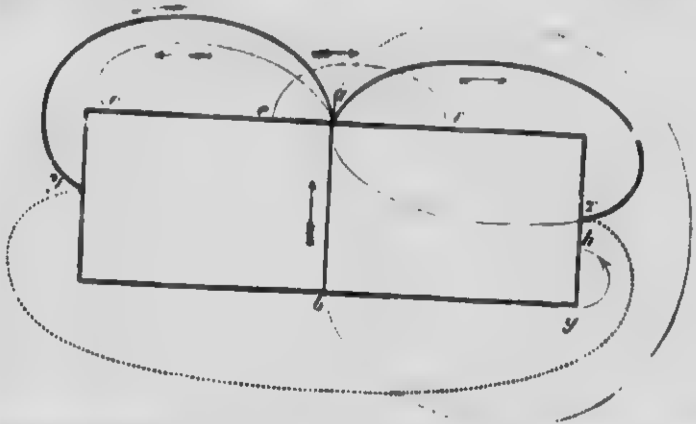

FIG. 80.—DIAGRAM ILLUSTRATING THE ELECTRIC CURRENTS OF REST OF MUSCLE AND NERVE (FOSTER).

Being purely diagrammatic, it may serve either for a piece of muscle or nerve, excepting that the currents at the transverse section cannot be shown in a nerve. The arrows show the direction of the current through the galvanometer.

a, b, the equator. The strongest currents are those shown by the dark lines, as from a at the equator to x or to y at the cut ends. The current from a to c is weaker than from a to y, though both, as shown by the arrows, take the same direction. A current is shown from e, which is near the equator, to f, which is farther from the equator. The current (in muscle) from a point in the circumference to a point nearer the centre of the transverse section is shown at g, h. From a to b, or from x to y, there is no current, as indicated by the dotted lines.

Muscle at rest and absolutely uninjured gives *no current whatever.*

If while the galvanometer is registering the direction of this injury current the muscle preparation be stimulated, a backward swing of the needle of the instrument towards zero indicates that the injury current is diminished; this diminution is termed the *negative variation.*

If an *uninjured* muscle, which is giving no currents, be stimulated into contracting activity, it exhibits electrical phenomena, the *current of action*, which account for the negative variation of the injury current. The causation of the action current is really of such a nature as to give rise to what is known as a *diphasic* variation in the current of a muscle, as shown by the needle of the recording galvanometer swinging first one way and then in the opposite direction. This double variation is due to the fact that the point on the muscle to which the stimulus is applied becomes negative to all points of the muscle at which the wave of contraction, resulting from the stimulation, has not yet arrived. This negativity arises during the 'latent period' (p. 360), and passes along the muscle as a wave which

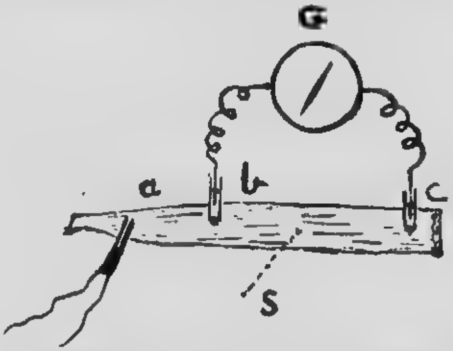

Fig. 81.—Sartorius Muscle arranged to Demonstrate the Diphasic Variation of Action Current in Muscle (or Nerve).

s, Sartorius; a, stimulating electrodes; b, c, non-polarisable electrodes as 'leads' to G, the galvanometer. The electrode c is intentionally not placed on the injured end of the muscle as it would be for demonstrating mere 'negative variation,' since the strong negativity of the injured end would mask the desired phenomenon. A similar arrangement suffices to demonstrate the same phenomenon in a piece of nerve.

precedes the wave of contraction. Thus if, as in Fig. 81, a muscle be stimulated at *a*, while the points *b* and *c* are connected through a very sensitive galvanometer, at the moment of stimulation *a* becomes negative to the rest of the muscle. As this negativity sweeps along the muscle it passes first over the point *b*, which thus becomes negative, and the needle of the galvanometer swings in one direction. Immediately afterwards it passes over the point *c*, and the needle swings in the opposite direction. Hence the diphasic variation.

These phenomena, while of the greatest interest in the case of muscle, become still more important in the case of a nerve, since they provide the only accurate means of following the passage of an impulse along a piece of *isolated* nerve, which does not, as does a muscle, change its shape or exhibit other obvious changes when stimulated.

The electrical phenomena in muscle are not an isolated example of electric currents in the body. Closely similar phenomena are demonstrable in nerves, and electrical changes, accompanying their functional activity, occur in secreting glands, in the eye, and to the highest degree in the electric organs of certain fish.

The Changes in Active and Resting Muscles.—The changes occurring in muscles are remarkably active. The processes which result in muscular contractions use up at every moment the combustible material of the structure, and the products arising from their metabolism have to be got rid of at once and repair brought about. Changes are also constantly occurring even during the period of muscle rest. Muscle activity is characterized by muscle waste, muscle rest is characterized by a preponderance of the process of repair; we must therefore learn the nature of the waste and repair occurring in muscles.

The oxygen carried to resting muscles by the blood is absorbed in considerable quantities, and a volume of carbon dioxide, in slightly less quantity than corresponds to the oxygen absorbed, is returned to the venous blood. Whether a muscle be at rest or active, it is always absorbing and storing up oxygen, and giving off carbon dioxide. The absolute amount of these varies; during work the oxygen used up and carbon dioxide produced are both increased, and the increase provides some measure of the work performed. Even during rest a muscle is doing work, for we have learnt that it is always in a condition of *tonus*, viz., of slight contraction. Since a muscular contraction is essentially the outcome of an oxidational process, the storage of oxygen by the resting muscle may be said, in Pflüger's words, 'to wind it up' in preparation for its contracting activity. This accounts for the fact that an excised muscle of the cold-blooded frog can be made to give some hundred contractions when suitably treated. In mammalian muscle, on the other hand, with its much greater metabolic activity, this quiescent storage of oxygen does not suffice to maintain its irritability for more than the briefest interval after its blood-supply is cut off.

In an active muscle the bloodvessels are more dilated than in the muscle at rest, and this dilatation provides for the increased quantity of blood now required by the part. By means of the blood the irritability of the muscle, or its power of contraction, is maintained; whatever leads to a smaller quantity of blood being sent to an active muscle, produces partial or complete paralysis of the group or groups of muscles affected. This is well seen in the horse when suffering from thrombosis of the iliac arteries; the blood-supply is sufficient during the time the animal is at rest, or even at a walk, but if called upon to trot muscular cramps occur followed by paralysis.

Our study of metabolism has prepared us for the statement that the chemical changes occurring during contraction do not normally affect the nitrogenous elements of the muscle. There is probably no increased output of nitrogenous substances such as creatine. The excretion of any increased amount of urea is variable, irregular, or even non-existent, and is in no case even remotely proportional to the work done. This is true as long as the body is supplied with a sufficiency of the non-nitrogenous carbo-hydrates and fats. If they are deficient, then increased muscular activity does lead to an increased formation of urea, since the muscle now has to metabolize its proteids to provide the energy necessary for the work performed and the heat simultaneously produced. The main products of muscular waste are therefore to be looked for in the destruction of stored-up carbo-hydrate material. Muscles in a state of activity contain less glycogen and sugar than those in a state of rest, due to the amount utilized during muscular activity; but glycogen is not necessarily the source of the energy, since muscles free from it work normally. During muscular activity heat is produced; the blood returning from a muscle has a higher temperature than that going to it. Colin found the temperature of the masseter muscle of the horse to rise 5° Fahr. through feeding. The whole body temperature in the horse is raised during work, and does not fall for some time after. In dogs a rise of temperature of several degrees may be obtained by stimulating the spinal cord, and thus producing muscular contractions.

A contracting muscle liberates energy in the form of both work and heat. We have seen reasons for regarding the oxidation of the non-nitrogenous carbo-hydrates as the normal source of this energy, and we have referred to the quiescent storage of oxygen during rest as accounting for the prolonged possible activity of an isolated frog's muscle. In connection with this it is not uninteresting to calculate, as Fick has done, the amount of carbo-hydrate necessarily oxidized to provide all the energy as work + heat furnished by a single maximally vigorous contraction of a frog's muscle. Knowing the heat of combustion of, say, glycogen, and converting the work of the muscle into heat by Joule's equivalent, we find that 1 gramme of frog's muscle can provide all the energy it sets free in a single maximal contraction by the oxidation of ·0006 milligramme of carbo-hydrate. In the case of fat the necessary amount would be still less, viz., ·00025 milligramme. This may serve to diminish our surprise at the working activity of which an excised muscle is capable.

Causation of a Muscular Contraction.—This is a problem as yet unsolved; our previous studies in every way point to the oxidation of carbo-hydrate substance as being the source of energy, and we have seen that it is impossible for a muscle to contract without using up oxygen and producing carbon dioxide. But we are now brought face to face with a paradoxical condition; if muscle be exposed to the vacuum of a gas-pump no free oxygen can be obtained from it, while if the ordinary nerve-muscle preparation be taken and placed in a jar of hydrogen it continues to contract, and, even still more remarkable, it continues to produce CO_2, though no oxygen exists in the atmosphere surrounding it! As CO_2 cannot be formed without oxygen, it is evident the oxygen must come out of the muscle, and to meet this difficulty it is supposed that the muscle molecules store up oxygen during rest in a hypothetical compound of hydrogen and carbon known as *inogen;* during muscular contraction this compound breaks down, and the waste products are liberated. The nature of the process by which the impulse conveyed to the muscle along its motor nerve becomes, through the agency of the end-plates, the stimulus which leads to this explosive compound being fired off as a muscular contraction is quite unknown. The nitrogen-holding substance in muscle is only used when the food-supply is insufficient or the work excessive; it is therefore the O_2 intake, and CO_2 output, which have to be examined in dealing with the question of the influence of muscular work on metabolism.

Fatigue.—Turning once more to the simple nerve-muscle preparation, it is found that if the muscle be kept at work the first few contractions, as shown by a series of tracings (see Fig. 82), may be progressively more vigorous. But if the stimulations are continued the muscle rapidly becomes fatigued, the latent period is lengthened, the height of each successive contraction becomes less and the duration of each contraction is prolonged, chiefly by a lengthening of the period of relaxation: the muscle, in other words, is in a state of fatigue (Fig. 82). We shall presently study fatigue from some other aspects, and will now only point out that the cause is here due to the using up of the contractile substance of the fibres and the accumulation in the muscle of the chemical products of contraction. In fact, if a fatigued muscle be washed out with normal saline solution and a little weak alkali circulated through its bloodvessels, it becomes restored, and regains its power of contraction. A muscle at work *in* the body is protected from ready fatigue by the ever-circulating blood, which supplies it with food and carries off the waste products of its activity.

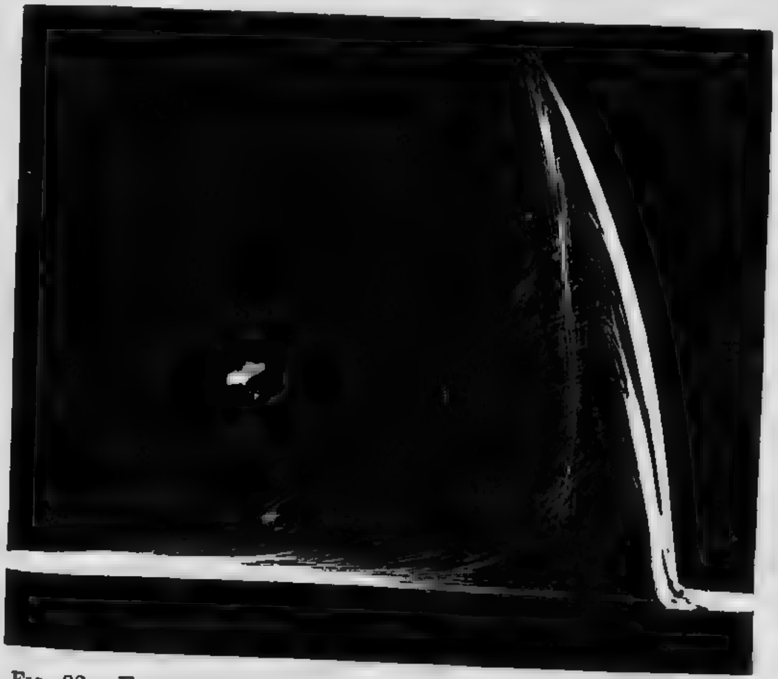

FIG. 82.—FATIGUE CURVE OF SKELETAL MUSCLE; GASTROCNEMIUS OF FROG (STEWART).

Time tracing $\frac{1}{100}$ of a second. The curve is read from right to left.

A muscle so fatigued by repeated stimulation may be restored by washing it out with physiological salt solution containing a little alkali; in course of time mere washing out of the muscle is not sufficient to ensure its recovery, but if serum or blood be transfused it is enabled again to start work. The material in muscles which gives rise to fatigue is probably sarco-lactic acid, and by passing a solution of this acid into muscles the typical phenomena of muscle-fatigue may be artificially induced. The production of potassium salts may also be a cause of fatigue, in spite of the fact that they are usually found in muscle, yet potassium salts in their action on this tissue rapidly destroy its irritability.

We have seen (p. 358) that muscles are connected by elaborated nerve-endings with sensory nerves, to whose existence the so-called 'muscular sense' is due. It is therefore conceivably possible that the sensation of general fatigue which arises from excessive muscular exertion is due to a cerebral appreciation of the changes brought about in the muscles as the result of their contracting activity. On the other hand, muscular activity implies the action of central nerve-cells in which the impulses which give rise to the contractions of the muscles are originated, of the passage of these impulses along the motor nerves, and of their communication to the contractile fibres by the agency of the end-plates. Hence the phenomena of fatigue, if we regard it as a 'weariness' of the body as a machine, may be really due to a fatigue of the central cells, of the motor nerves, or of the end-plates. We may at once dismiss the motor nerves from our consideration inasmuch as nerves do not appear to be capable of fatigue (p. 385). Now the blood of a fatigued animal contains fatigue products, and if it be transferred into the circulation of a normal animal, all the symptoms of fatigue are produced. If the spinal cord be divided and the distal end stimulated, the hurried respiration of fatigue may be produced as the result of muscular contractions (see p. 118). Possibly, therefore, the phenomena are due to the injurious action of the products of muscular activity on the central motor nerve-cells, and some experiments on men go to show that the central nervous system is readily affected by fatigue products. On the other hand, recent work by Wedenski opens up the possibility that fatigue, if we look upon it as an inability to drive the muscular machinery up to its normal capacity, may be due to the deleterious influence of the products of muscular contraction on the end-plates. This view receives support from the fact that a fatigued muscle will contract by *direct* stimulation when it refuses to respond to a stimulus brought to it through its nerve.

Elaborate experiments on man performing muscular work show how readily the intake of O_2 may be increased; such causes as difficulties in the road, rising ground, increase in pace, change in the load carried, unpractised movements, even a sore foot, may increase the consumption by 18 per cent. Fatigue produces wasteful metabolism, and may increase the CO_2 excreted even as much as 21 per cent. The abnormal use of certain muscles, such as a man with sore feet would employ in order to save himself pain, produces extravagant combustion and fatigue. What applies to man in these matters applies equally to the horse; ungreased axles, badly-fitting harness and saddlery, badly-made roads, sore backs and lameness, all represent undue muscular wear and tear.

Condition.—That remarkable state of the body described as 'condition,' into which horses can be brought by care in feeding, general management, and carefully regulated work, must be regarded as the highest pitch of perfection into which muscles can be brought. In its highest degree it is not a permanent state; no horse can remain in it for any length of time, and many can never be got into condition for severe work. It is easy in the training of horses to overstep the mark and produce 'staleness,' a result which is usually recovered from by a short judicious rest, to which the system immediately responds.

During training all superfluous fat and water are removed from the body, the muscle substance is built up, and the respiratory capacity increased; but it is very necessary to remember that condition, though judged of largely by the state of the muscles, has a very important claim on the respiratory and circulatory systems. To sustain severe and prolonged muscular exertion an adequate supply of oxygenated blood must be sent to the muscles; this necessitates a rapid flow of blood and adequate ventilation in the lungs, with strong regular pumping power in the heart; all these factors must work in harmony. As a matter of fact the ability to endure the strain of a violent muscular effort is far more dependent on the training of the respiratory and cardiac mechanisms than on that of the muscles. Long walking exercise is given as a muscle developer, and judicious gallops to give an animal its 'wind,' yet as a matter of fact the 'wind' is largely a question of heart. As the circulatory pump works at high pressure the bloodvessels must be fit to stand the strain, and to return to the heart at both auricles the amount of blood leaving by both ventricles. A deficiency in this mechanism leads to 'loss of breath'; clogging in the lungs means deficient oxygenation in the tissues, and without an adequate supply of oxygen the muscles are powerless to contract. We are clearly shown, from what may be witnessed in the hunting-field, or wherever horses are exposed to long-continued strain, that the chief value in training is located in the functional improvement of the muscular tissue of the heart and in the circulatory system in the lungs; both of these have to be educated to withstand the extra strain imposed and to work economically. The voluntary muscles have also to be educated to work in the best and most economical manner; they must be used to advantage, smoothly and in combination; their response must increase in rapidity and power, while their relaxation must not be too prolonged and so cause loss of time. Unpractised movements are a serious source of waste; by practice the same amount of work can be performed with a reduced expenditure of energy, and this is true for both men and horses.

There is additionally another factor of supreme importance in training. The respiratory movements, as we have learnt, are dependent upon the rhythmic activity of the respiratory centre (p. 108). Hence this centre must be taught to withstand the extra strain imposed upon it during violent exertion. What the centre has to 'learn' in respect of this is more or less a matter of conjecture. Bearing in mind the powerfully stimulating influence on the respiratory centre of the waste products of the metabolism involved in muscular contraction, it is conceivably possible that 'wind' is the result of an increased immunity of the centre to the action of these products. However this may be, one thing is certain—namely, that respiratory distress is more potent than most other factors in determining 'staying power,' the one thing to which all long-distance athletes strive to attain. In this connection we may point out that it is said that the deleterious products of metabolism produced during fatigue may be neutralized and immunity established by giving small doses of extracts of a fatigued muscle; the question has therefore arisen as to whether 'training' is a process of immunizing against fatigue products?

Chemical Composition of Muscle.—A dead muscle does not possess the same chemical composition as one which is living, and we cannot analyse living muscle without killing it by the methods necessarily employed. Thus any tabular statement of the quantitative composition of muscle gives really the composition of dead muscle. We are, however, assisted to some knowledge of the nature of living muscle-substance by the following facts.

If contractile, and therefore living, frog's muscle is carefully frozen and then very slowly thawed, it does not lose its irritability: it is still alive. When frozen it may be minced with a cold knife and ground up in a cold mortar with four times its weight of snow containing 1 per cent. of sodium chloride. By this process a viscid liquid is obtained which may be filtered, though with difficulty, at 0° C. The fluid filtrate is opalescent, neutral, or faintly alkaline in reaction, and is known as 'muscle-plasma.' When its temperature is allowed to rise it coagulates in the same way as does blood-plasma, yielding a *clot* which, unlike fibrin, is granular and flocculent, and forming a liquid *serum*. During the clotting the liquid becomes acid, as the result of a formation of *sarco-lactic acid*, and the clot consists of *myosin*. Assuming, as we may reasonably do, that the muscle-plasma represents more or less closely the muscle-substance in the living fibre, we may take these phenomena of the clotting of the muscle-plasma as indicating the most characteristic chemical differences between living and dead muscle (though there are others), and thus we gain considerable insight into the composition of living muscle as based upon an analysis of the dead tissue.

With this preliminary caution we may now state the composition of muscle to be approximately as follows:

Water - - -	75 per cent.
Proteids - - -	20 ,,
Fat - - - -	3 ,,
Carbo-hydrates - -	·4 to 1 per cent.
Nitrogenous waste products -	·2 ,,
Salts - - - -	1 to 1·5 ,,

Our knowledge of the nature of the proteids of muscle is a matter of no slight uncertainty, which is not made less by the existing confusion in the terminology employed by various investigators. Into this we cannot here enter. It must suffice to say that the chief and characteristic proteid of dead muscle is the *myosin* formed in the clotting of muscle-plasma; it belongs typically to that class of proteids known as *globulins*. Bearing in mind the phenomena of the clotting of muscle-plasma and using the nomenclature employed for blood-plasma, we may say that living muscle contains *myosinogen*, which on the death of the muscle is converted into myosin, just as in blood-plasma fibrinogen gives rise to fibrin (p. 18). It has not as yet been shown that calcium salts play a part in the coagulative formation of myosin, as they necessarily do in case of fibrin and of the casein-clot in milk. The proteids of living muscle are not entirely myosinogen, nor are those of dead muscle entirely myosin. Other members of the globulin class are present in both, as also an ordinary albumin closely resembling serum-albumin.

The carbo-hydrate material is composed chiefly of glycogen, which diminishes in amount, by conversion into sugar, on the death or after the contracting activity of muscles; these substances have already been fully dealt with in a previous chapter. The nitrogenous waste products or 'extractives' are creatine, hypoxanthine, xanthine, carnine, taurine (in horse-flesh), uric acid in minute traces (though more abundant in reptilian muscle), and traces of urea, though this is a question still not decisively settled; of these creatine is by far the most important. It is a substance we have already studied in connection with the production of urea (p. 295). The ash in muscle consists principally of the salts of potassium and phosphoric acid. The gases are carbon dioxide, together with a small amount of nitrogen but no free oxygen.

Rigor Mortis.—After death a muscle passes into the condition of rigor or stiffening, by which it changes both in its physical and chemical aspect. The muscle becomes firm and solid, loses its elasticity, and no longer responds to electrical stimuli; further, it loses its alkaline reaction, and in course of time becomes acid owing to the formation of sarco-lactic acid. Through the death of the muscle its proteids coagulate, and this process is generally believed to be identical with the clotting of muscle plasma previously described. Rigor mortis and the production of sarco-lactic acid are closely connected, so that if the formation of the acid be prevented by suitable means, rigor does not occur. The view now adopted as to the cause of death stiffening is that it is due to a coagulation of the proteids by the products of metabolism in the muscle, and this explanation accounts for the rapid setting in of rigor in animals hunted to death. Rigor mortis is delayed in a rabbit in which the labyrinth of the internal ear has been destroyed. This is probably connected with the obscure problem of muscle tonus, with which the labyrinth is connected. The muscles in which delayed rigor mortis occurs are those corresponding to the same side of the body as the injured labyrinth. During rigor mortis CO_2 is produced and heat evolved; some after-death temperatures are remarkably high. After a certain length of time rigor mortis passes off and decomposition commences. It is doubtful whether rigor mortis occurs in involuntary muscle: the appearance presented in this variety of muscle may be due to cold, for it has been shown that two or three days after death smooth muscle may be warmed up so as to be capable of contraction.

Phenomena of Contraction in Smooth Muscle.—Though there is a marked difference in appearance between red and white muscle, the actual phenomena of contraction do not differ excepting in the matter of rate. The latent period, contraction, and relaxation, are present as in red muscle, but occur more slowly; they are, in fact, sluggish and deliberate. Owing to the existence of numerous nerve fibres and ganglia, white muscle may be completely isolated from all nervous connections, and still continue to exhibit the phenomena of muscular contraction.

In response to a continuous or induced current pale muscle behaves much as does red, excepting, of course, that the response is slower. Summation also is present, though not identical with that observed in red muscle, for no contraction follows the first three or four stimuli; it is the stimuli which here accumulate before contraction follows, and after this has occurred the muscle subsequently responds to further stimuli by an increased height of contraction as does a red muscle.

Mechanical stimulation of pale muscle excites a sluggish but marked response; pinching the intestines produces peristalsis, and even drawing the finger lightly over the stomach wall may produce 'weals' of contraction. The muscle is markedly responsive to tension, resembling in this a skeletal muscle which up to a certain 'load' does more work the greater the weight it has to lift. Thus a frog's gastrocnemius, loaded successively with 10, 30, and 90 grammes, will do work proportional at each contraction to the numbers 106, 312, and 760·5. In the case of the digestive canal this is probably the chief source of stimulation, and in this connection we may call to mind the influence of cellulose in the diet of the herbivora (p. 207), the bulkiness of their food providing the mechanical stimulation and the distension necessary to produce the tension to which pale muscle is so responsive. The same remark may also apply to the physiological action of the stomach and intestinal gases; nor must the bladder be omitted from this consideration, from the point of view that distension by fluid provides a tension of the walls which acts as a stimulus to contraction.

CHAPTER XIV

THE NERVOUS SYSTEM*

Nerves.—Various classifications have been adopted for nerves. Anatomically they are known as cranial, cerebrospinal, and sympathetic, but for physiological purposes they are classified according to their function. From a structural point of view there are (1) medullated, (2) non-medullated nerves. Classified according to their function there are (1) afferent, frequently called sensory, and (2) efferent, commonly called motor. The division into motor and sensory is so obviously incomplete, confining the function of nerves simply to the conveyance of motor impulses, or of those which give rise to sensation, that the terms afferent and efferent are better.

Afferent nerves are those conveying an impulse from the periphery of the body to a nervous centre, that is to say conveying centripetal impulses. The centre may be situated in the brain or spinal cord, and the impulses thus conveyed may be those of (*a*) special sense such as sight, hearing, taste, smell, etc.; (*b*) impulses producing sensation pleasurable or painful, from skin, muscle, and viscera; (*c*) impulses producing the impression of heat and cold, or (*d*) impulses leading to a reflex act without affecting consciousness at all.

Efferent nerves are those conveying impulses from a centre to the periphery, that is conveying centrifugal impulses; these impulses in the main are of a motor nature evoking from the muscles, bloodvessels, and viscera movements and contractions; they may also be of an inhibitory or controlling character, such for instance as the impulses which slow the heart, dilate the bloodvessels, or restrain the peristaltic contraction of the bowels. But besides these, centrifugal impulses may be of such a nature as to cause glands to secrete, or to regulate the metabolism of a part, or control, stop, or augment other of its actions.

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* My best thanks are due to Professor Sherrington, F.R.S., for reading this chapter, and kindly supplying that portion of it dealing with "stepping" and the "scratch reflex."

Structure of Nerves.—Medullated nerves, often spoken of as white nerve-fibres owing to their colour, are distinguished microscopically by the fact that their component fibres possess a white fatty sheath enveloping the essential nerve-substance or *axis-cylinder*, which lies like a core within it. The axis-cylinder is the true nerve-substance, and is in connection with either the brain or spinal cord, depending upon the position of the nerves. In these organs cells with processes are situated; one of the processes becomes the axis-cylinder of a nerve, so that some of the cells of the brain, and especially of the spinal cord, may be looked upon as possessing processes of immense length. The white fatty sheath, known as the *medullary sheath*, which covers the axis-cylinder does not extend continuously along the nerve, but is broken at intervals termed *nodes;* the portion of nerve-fibre included between two nodes has somewhere in it a nucleus. It is at the nodes, where the fatty sheath is absent, that the material which supplies the nerve with nutrition gains access. Covering the medullary sheath is a delicate membrane which envelops the fatty matter, and is known as the *neurilemma.* Such is the structure of a single nerve-fibre; bundles of such fibres, enclosed in an appropriate sheath of connective tissue, constitute a nerve.

The non-medullated nerves, often spoken of as sympathetic or grey fibres, possess no white fatty cover around their axis-cylinder; they are freely nucleated at intervals, and made up in bundles as are the medullated nerves.

The essential feature in the nerve is the axis-cylinder; it is the true impulse-conducting substance, while fatty sheaths can only be looked upon as a means of insulation or support. From what has been stated about the nature of the axis-cylinder, it can be readily understood that every nerve runs direct from its origin to its termination, there is no union of nerve-fibres, each and every one is distinct, though numerous divisions may exist at their termination. In certain cases medullated nerves enter nervous bodies known as *ganglia* and leave them as non-medullated fibres. All medullated nerves before breaking up in the tissues they are intended to supply lose their fatty sheath and eventually their neurilemma, nothing but the bare axis-cylinder being left.

Ganglia on Nerves.—Placed on certain nerves, somewhere in their course, are masses of nervous tissue called ganglia; these ganglia are composed of an outer covering of connective tissue enclosing nerve cells, between which nerve-fibres pass; the cells are of a particular shape depending upon whether the ganglion examined be from the cerebro-spinal or sympathetic system. In the former the nerve cells are round and possess a projection or pole, which not unfrequently coils before issuing from the cell, and after running a short distance divides T-shaped into two branches which travel in opposite directions; such a body is known as a unipolar cell. The ganglia belonging to the sympathetic differ in the shape of their cells, for these instead of having one pole like the cerebro-spinal, have two, three, or more poles, known as bi-polar or multipolar cells. We may here say, though the subject will be touched on again, that the cells of the brain, spinal cord, and sympathetic system, are mainly multipolar, whilst those of the spinal and cranial ganglia are unipolar. Bi-polar cells may be found in the spinal ganglia of fishes. One process of a nerve-cell is the axis cylinder of a nerve, the other processes branch, dividing and subdividing like a root, and become primitive fibrils.

Nerves are remarkable for their want of elasticity; they do not retract on being divided; further they are capable of very considerable stretching without breaking. In the human subject the nerves of the limbs require a weight of from 40 lbs. to 120 lbs. to break them. There are nerves supplying nerves, the *nervi nervorum*, and the rationale of nerve-stretching in painful diseases is probably accounted for by the damage done to these minute nerves during the process.

Nerve trunks receive a poor blood supply, though ganglia and grey matter are richly vascular; it is possible that the numbness produced in a sensory nerve by pressure is due to its blood supply being temporarily cut off, the nerve thus losing its irritability. The lymphatics are numerous, and exist within the lamellæ of the perineurium or covering of the nerve bundle.

Excitability.—We have no means of distinguishing microscopically between an afferent and an efferent nerve; there is nothing in the structure of a motor, sensory, or secretory nerve, which enables its function to be determined. Further, we know that though in the body impulses pass only in the one direction through a nerve, yet removed from the body and tested electrically it is as easy to pass impulses in one direction as another. Nerves however are excitable, the living nerve can be made to react by means of chemical, mechanical, or electrical stimuli, and when so excited appears to transmit the same impulses as when irritated physiologically, viz., as when the normal body impulses are being transmitted; thus the stimulation of a sensory nerve gives rise to pain, of a motor nerve to muscular contraction, and of a secretory nerve to secretion. The conductivity of nerves is diminished by cold, compression, or injury, but it is noteworthy that even after long-continued excitation nerves are found practically unfatigued. Impulses are no longer transmitted when nerves are ligatured or divided.

Electric Phenomena of Nerves.—Some very definite facts are known in connection with the electric currents in nerves, and the effect on the excitability of the nerve of transmitting currents through it; these facts have been ascertained with the nerves of the frog, and so far as can be proved apply equally to those of the higher animals.

If a nerve be removed from the body and suitably applied to an instrument which is capable of measuring delicate electric currents, the galvanometer, the needle of the instrument will be found to be deflected, showing the passage of a current; it is spoken of as the *current of rest*, but it does not exist in uninjured nerves. It is practically identical in direction with the natural muscle current described on p. 367. If while the current of rest is passing shocks be sent into the nerve from an induction coil, the needle of the galvanometer is found to indicate a momentary current in the opposite direction to the current of rest. This momentary opposite current is spoken of as *negative variation* or the *current of action*, and the phenomenon is essentially the same as in the case of a muscle.

The negativity developed at the point to which the stimulus is applied travels as a wave in both directions along the nerve at the rate, for frog's nerve, of about 28 metres or some 90 feet per second. In the case of a muscle the change of shape when stimulated provides the necessary indication of its receipt of an impulse. Not so with a nerve. Here we have no change of shape, no development of heat, to mark its functional activity. The *one* indication of the passage of an impulse along an *isolated piece* of nerve is the electrical change taking place in it, and hence the study of the 'current of action' and the onward rush of the attendant 'negativity' is here of supreme interest.

Turning next to the nerve-muscle preparations suspended in the moist-chamber (see p. 359), and using the contraction of the muscle as an index of the activity of its nerve, we may study other important phenomena of nerve-excitation. If a moderately strong constant current be passed into the nerve by connecting it with the poles of a battery, at the moment the connection is made the muscle gives a twitch or contraction, and then remains perfectly quiet though the current is still streaming through its nerve; if the connection be broken as by opening a key in the battery circuit, the muscle gives another contraction. These are termed 'making' and 'breaking contraction,' viz., a contraction produced on closing and opening the electric circuit. If instead of a moderately strong constant current a weak or very strong one be used, the results on making and breaking may not be the same.

During the period of apparent quiescence following the closing of the circuit, though the muscle is giving no indication of the current, yet changes are occurring in the nerve. If it be tested by stimulating it with an induced current, it is found that its irritability, as measured by the greater or less contraction of the attached muscle, is diminished in the neighbourhood of the positive pole (anode) of the continuous current, and increased in the neighbourhood of the negative pole (kathode). This changed condition is known as **electrotonus**, the diminished irritability being known as **anelectrotonus**, the increased excitability as **kathelectrotonus**. Between the increased and reduced irritability is a zone of unaffected irritability known as the **neutral point**. During the condition of electrotonus there is no interruption to the natural nerve current, which is simply increased in strength if the constant current takes the same direction in the nerve as the current of rest; but if the constant current be passed in the opposite direction to the nerve current, the latter is diminished.

A reference to Fig. 83 will suffice to make the matter clear. At a certain part of the nerve a continuous current of electricity generated at E is passed through it, the application and withdrawal of which gives rise to the making and breaking contraction previously mentioned; during the passage of the current the muscle is perfectly quiet, in spite of important changes occurring in the nerve. Shocks are now sent into the nerve from an induction coil at a place between the muscle and the points of application of the continuous current; as the result of the stimulation the muscle either responds more than it should do for the strength of the stimulus employed, viz., there is increased excitability of the nerve (kathelectrotonus), or the muscle does not respond as strongly as it should, viz., there is decreased excitability of the nerve (anelectrotonus). The increase or decrease of excitability in the nerve depends upon whether the continuous current is passed down it,

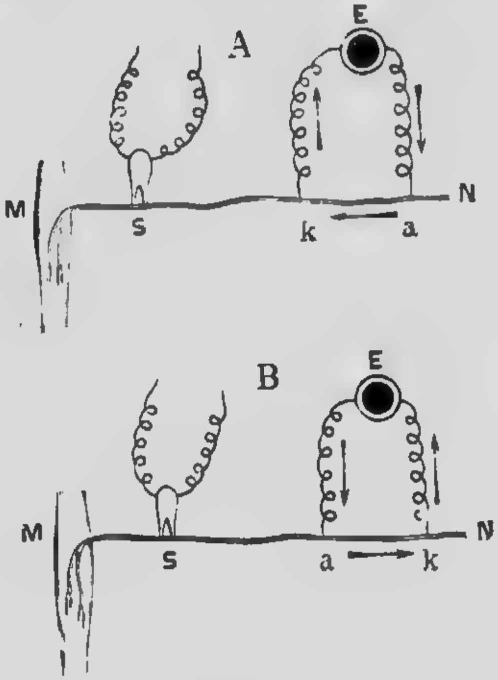


Fig. 83.—Diagram of Electrotonus.

N, The nerve running to the muscle M; E, battery or cell for the production of a constant current, the positive pole or anode (a) in A being placed furthest from the muscle, the current consequently flowing down the nerve, and in B being placed nearest to the muscle, the current flowing up the nerve. At S the nerve is stimulated by an induced current, and its irritability determined by the contraction of the muscle M; the irritability is increased in A, kathelectronus, and decreased in B, anelectrotonus.

as in A, or up it, as in B; with a descending current the excitability is increased, with an ascending one it is decreased.

The explanation of electrotonus in nerves is that it is a vital phenomenon, viz., the irritability of the nerve is increased when its molecules pass from their ordinary condition to one of greater mobility (kathelectrotonus), or it is diminished when its molecules pass from their ordinary condition to one of less mobility (anelectrotonus). Hermann considers that it is a purely physico-chemical phenomenon, due to the electric current generating acids at the positive pole, and alkalis at the negative; the effect of the acid is to lower the excitability of the nerve, and of the alkali to increase it. One practical application of this law is that the excitability of a part, as in pain, cramp, etc., may be removed by passing a current up the nerve, viz., by placing the positive pole nearest the muscle, and producing anelectrotonus; or by reversing the process and throwing the current down the nerve, so that the negative pole is nearest the muscle, the irritability of the part may be increased.

The Nature of Nervous Impulses is quite unknown, excepting that they travel in the form of a wave of electric disturbance, which is shorter, and travels more rapidly than that which traverses a muscle. Impulses are not transmitted from one fibre to another in a nerve bundle.

Conductivity of Nerves.—Compared with electricity a nervous impulse travels very slowly, and it is necessary to bear this in mind as comparisons between electric currents and nerve impulses have been made. The velocity of nervous impulses in motor nerves has been stated to be between 111 to 140 feet per second, whilst through sensory nerves it is said to be faster, 160 to 320 feet per second; in visceral nerves the velocity is less. Chauveau ascertained in the pharyngeal branches of the vagus that the velocity amounted to 26 feet per second.

Degeneration of Nerves.—When nerves are cut they degenerate, the degeneration always taking place in the portion cut off from its nutrient centre. The nerve fibre, as has been stated above, is but a branch of a nerve cell; if a portion of a cell be separated from the part containing the nucleus of the cell it soon dies. Thus, when a large amœba, or a Radiolarian, is torn up into several pieces, the portions containing no nucleus degenerate and die; but that portion containing the nucleus repairs itself and reforms a perfect cell. The nerve fibre dies down after being cut, just in so far as it is a piece of cell cut off from its nucleus. The sensory nerve divided in neurectomy, as practised on the horse, degenerates towards the foot and not up the limb, for it is the piece below the wound which is cut off from its nutrient centre and not the portion above; had this been a motor nerve the degeneration would still have taken place below the wound and for the same reason. All spinal nerves have their seat of nutrition either in the spinal cord or in the ganglia just outside it (see p. 384); the nearer to the spinal cord the point at which the section is made the greater the length of nerve which degenerates, the further away from the cord the point at which section is practised the shorter the length which degenerates. When the nerve degenerates the fatty medullary sheath breaks up, forming globules around the axis-cylinder; the latter also degenerates and ultimately breaks up. The remarkable fact about these changes is the rapidity with which they occur, six days is sufficient to show their commencement; small nerve fibres degenerate more quickly than large.

By suturing divided nerves union occurs, and though the act of division causes degeneration, yet when union takes place regeneration of fibres occurs; a fresh axis-cylinder grows through the length of the degenerated nerve, and after some weeks and often months motion or sensation is restored. the former always much later than the latter. Even suture of divided nerves is not always necessary for union; we know clinically that the plantar nerves of the horse will often unite in a few months in spite of a piece being excised, the portion of nerve above sending down an axis-cylinder which soon finds out its divided portion below.

Not only is the nutrition of the nerve itself affected by nerve division, but also the nutrition of those parts supplied by it. Ulceration more or less severe has been known to follow injury of certain nerves; sloughing of the cornea occurs in animals when the ophthalmic division of the fifth is divided; and many are practically acquainted with the sloughing of the entire foot which sometimes, though fortunately rarely, follows the operation of neurectomy. It is undoubted that nerves influence the nutrition of a part; nowhere is this better demonstrated than in cases of intense muscular atrophy due to nerve injury.

Nerve Terminations.—There are some structures such as glands where the nature of the nerve termination is not satisfactorily made out, there are other places such as muscle where definite and distinct motor nerve-endings have been found; and on many sensory and sympathetic nerves special terminations known as Pacinian corpuscles and Krause's end-bulbs exist. Nerve terminations are found in the muzzle of animals, in tendons, in muscles, in the generative organs, conjunctiva, mouth, tongue, epiglottis, etc.; some are known as Krause's end-bulbs, those in tendon are described as the organ of Golgi, in muscle they are known as end-plates, whilst in the skin of the muzzle the nerves terminate in small swellings or enlargements known as tactile cells, which are placed between the epithelial cells of the epidermis; cells of this kind also exist in the foot of the horse. The nerves of special sense have each a distinct termination peculiar to themselves, such as the hair cells of the internal ear, the rods and cones of the retina, taste bulbs of the tongue, etc.

Spinal Cord.

The spinal cord extends from the atlas to about the second or third sacral vertebra, and is completely enclosed in a dense membrane, the dura mater. The canal in which it is lodged is very much larger than the cord, especially at those parts where the greatest amount of movement occurs, as in the neck. The cord is not the same shape nor the same size throughout; oval in the cervical region, it becomes circular in the dorsal, and again oval in the lumbar portion. It is largest where any considerable bulk of nerves is being given off, and thus there is an enlargement corresponding to the fore, and another to the hind limbs. On exposing the spinal canal, a large number of nerves are found to be passing through the dura mater either outwards or inwards, and these gain an exit from or entrance to the spinal canal by means of the foramen formed at the junction of the vertebræ.

Spinal Nerves.—On opening the dura mater, it is observed that the nerves divide in such a way that one part of each of them runs to the superior, and the other part to the inferior surface of the cord; these are spoken of as the superior and inferior roots of the spinal nerves. In the horse each superior and inferior root enters the cord not as a single cord but as several. On the superior root, but outside the dura mater, is found a ganglion; each rootlet of a superior spinal root has a ganglion on it: no such body exists on the inferior root. Both inferior and superior roots unite below the ganglion to form a mixed spinal nerve (see Fig. 84). The function of these two roots is entirely different; the superior root, possessing the ganglion, conveys centripetal (sensory) impulses only; the inferior root conveys centrifugal (motor) impulses to muscles and glands. The superior roots are passing into the cord, the inferior roots are passing out of it.

Passing out with the inferior root of the spinal nerve, but indistinguishable from it, is a branch of nerve known as the white ramus communicans, which leaves the main trunk after the mixed nerve has been formed, and runs to a distinct system known as the sympathetic. One part of the latter, the gangliated cord, runs under the arches of the ribs and back as far as the loins; to this cord the white ramus runs, and establishes a communication between the cerebrospinal and sympathetic system; in this branch are, among others, the nerves which constrict the bloodvessels. A careful study of Fig. 85 is necessary for the clear elucidation of the arrangement of the spinal nerves.

Arrangement of the Cord.—If a cord be suitably prepared, a transverse section shows that it consists of two similar halves, united by a comparatively small central mass of tissue through whose centre a minute (longitudinal) canal runs. The halves are separated by fissures on the superior and inferior surfaces of the cord: the inferior fissure is wide and does not reach down to the centre of the cord, while the superior fissure is narrow and deeper (Fig. 84). Each half is further seen to consist of a superior, lateral, and inferior column, separated from each other by a shallow longitudinal groove.

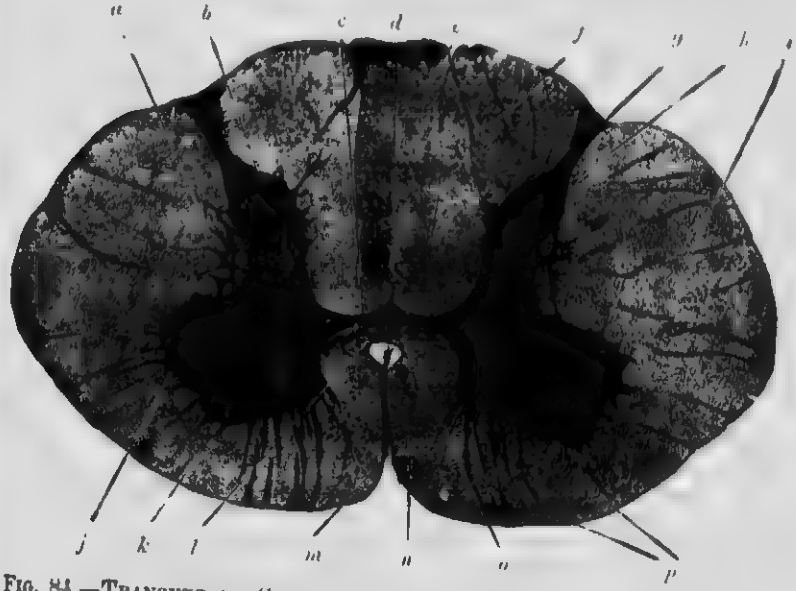
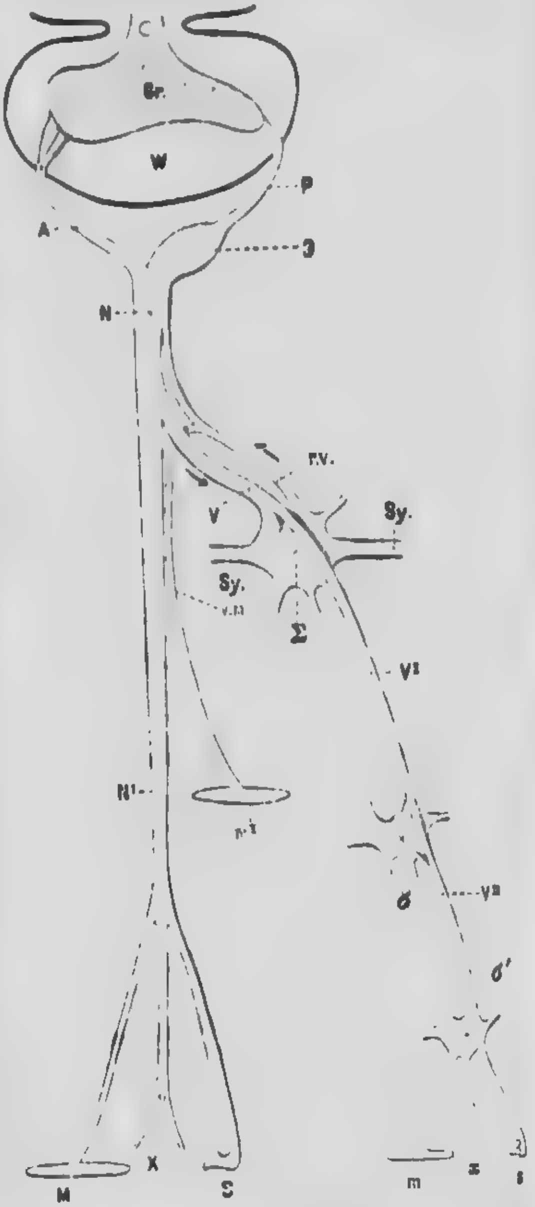


FIG. 84.—TRANSVERSE SECTION OF THE SPINAL CORD IN THE CERVICAL REGION ×8D. THE LINES IN THE LATERAL AND SUPERIOR COLUMNS RUNNING FROM THE OUTER MARGIN ARE LAMINÆ OF THE PIA MATER (M'KENDRICK).

a, Processus reticularis; *b*, superior horn; *c*, grey commissure; *d*, superior septum; *e*, Goll's column; *f*, superior column; *g*, point of entry of superior root; *h*, substantia gelatinosa; *i*, lateral column; *j*, large multipolar nerve cells; *k*, inferior horn; *l*, white commissure; *m*, inferior longitudinal fissure; *n*, inferior column; *o*, central canal; *p*, point of exit of inferior roots.

A section of the cord shows it to be made up of both white and grey matter; the latter placed internally, and forming the medulla, is arranged something like two commas placed back to back, the tail of the comma being uppermost. The tail of the comma corresponds to the incoming sensory

FIG. 85.—SCHEME OF THE NERVES OF A SEGMENT OF THE SPINA CORD (FOSTER).



Gr., grey; W, white matter of spinal cord; A, inferior; P, superior root; G, ganglion on the superior root; N, mixed nerve, consisting of sensory and motor branches with fibres passing into the sympathetic system at V; N^1, spinal nerve, consisting of sensory and motor branches, terminating in M, skeletal muscles, S, sensory cell or surface, and X, in other ways. V, white ramus communicans uniting the cerebro-spinal with the sympathetic system; it runs out from the cord with the inferior spinal nerve, and is given off from the mixed nerve at V, from whence it passes to Σ, a ganglion on the sympathetic chain, and thence on to V^1 to supply the more distant ganglion σ, then to V^{11} to the peripheral ganglion δ', and ends in *m*, a visceral muscle, *s*, a visceral sensory cell or surface, and *x*, other possible visceral endings.

From Σ is given off a branch, r.v., known as the grey ramus communicans, which partly passes backwards towards the spinal cord and partly runs, as v.m., in connection with the spinal nerve to supply vaso-constrictor fibres to the muscles of bloodvessels, m^1, in certain parts, for example, in the limbs.

Sy, the sympathetic chain (gangliated cord of the sympathetic) uniting the ganglia of the series Σ. The terminations of the other nerves arising from Σ, σ, σ', are not shown.

fibres, the head of the comma to the outgoing motor ones; the two commas anatomically known as cornua are connected by a band of grey matter called the grey commissure, in the centre of which is a canal. The white substance of the cord is not of the same thickness throughout; stated generally the cord increases in white matter from the tail to the head; the grey matter is largest in the cervical and lumbo-sacral enlargements, and this increase and decrease in size corresponds with the increase and decrease in the number of nerves entering and leaving the cord in these regions. The white substance of the cord is found microscopically to consist of longitudinally arranged medullated nerve fibres, very much like those previously described, excepting that the fatty white substance has not the same covering found in other medullated nerves, but is enclosed in a sheath of neuro-keratin which is peculiar to the spinal cord. Between the groups of fibres peculiar branched corpuscles exist known as glia cells; these belong to a connective tissue peculiar to the cord, called the *neuroglia.*

The grey matter of the cord consists of cells, many being large and multipolar; amongst these are very fine fibres, either the delicate processes of the cells, or of medullated or non-medullated fibres derived from the white substance of the cord, and terminating in the grey matter: the whole is held together by neuroglia. The nerve cells of the grey matter of the inferior cornua arrange themselves into certain groups in various parts of the cord, those situated at the lower part of the cornua run the entire length of the cord, but others are limited to certain regions, being at some parts strongly in evidence, at others almost or entirely absent. The cells are very large, and possessing numerous branched processes or poles, are known as multipolar cells. In the superior cornua the cells are not in groups, and moreover they are much smaller.

A peculiar column of cells known as Clarke's column is limited to three portions of the spinal cord; the cells are found lying above the inferior cornua towards the middle line of the cord, and are related to the endings of sensory nerves entering the cord. The cells of this column have few processes, and their long axis lies in the long axis of the cord.

Distribution of Nerve Fibres in the Cord.—The superior spinal nerve root joins the superior cornu, the inferior proceeds from the inferior cornu. We must now learn how the fibres composing these roots are disposed with reference to the cord itself. The fibres of the superior spinal nerve root grow from the spinal ganglion, enter the superior column of the white matter of the cord, and some travel forwards, others backwards in its substance. After running a short distance the fibres bend at right angles, enter the grey substance of the cord, and end not

FIG. 86.—LATERAL COLUMN OF A NEW-BORN RABBIT TO SHOW THE COLLATERAL FIBRES, AND THE MANNER IN WHICH THE LONGITUDINAL FIBRES BEND ROUND AND END FREE IN THE GREY MATTER (LANDOIS AND STIRLING, AFTER RAMÓN Y CAJAL).

c, Collateral fibres ; *cl*, bending round of the longitudinal fibres ; *l*, to end in the grey matter ; *n*, axis cylinder process of nerve-cell bending in amongst the longitudinal fibres of the white column.

in nerve cells but simply in fine branches (Fig. 86). During their course, before the final bending occurs, they all give off *collateral* fibres at right angles to the main trunk, which enter the grey matter, and connect the parent fibre with various segmental levels of the cord.

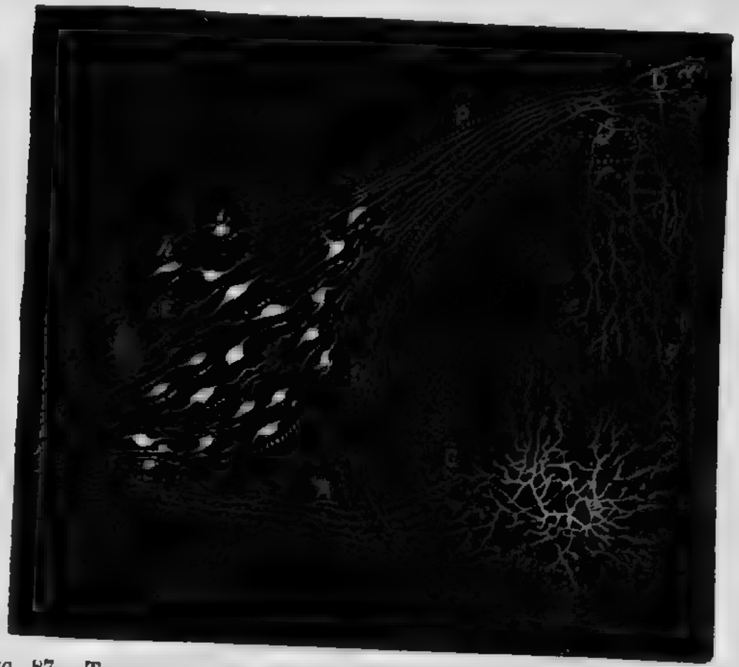


Fig. 87.—Transverse Section of the Spinal Cord in the Thoracic Region of an Embryo Fowl, at Ninth Day of Incubation (Landois and Stirling, after Ramón y Cajal).

A, inferior root; P, superior root of spinal nerve; C, axis-cylinder of a motor nerve-cell, issuing from the large cells of the inferior cornu; D, intra-medullary part of the superior root; *e*, origin of a collateral branch, which ramifies as *f g*, the terminal ramifications of the collateral fibres; *d*, final bifurcation; E, ganglion on superior root; *h*, bipolar ganglionic cells; *i*, a unipolar nerve-cell similar to those in mammals.

In this way all the sensory fibres reach the grey matter of the superior and in some cases the inferior cornua, terminating in numerous fibrils close to but not in continuity with the nerve cells (Fig. 87). The superior column of white matter is made up entirely of the fibres of the superior roots arising in the cells of the spinal ganglion.

The fibres of the inferior spinal nerve roots may be traced into, or rather, out of, the grey matter of the inferior cornua. There each has its origin, for it really arises in one pole of the large multipolar cells situated there, the remaining poles of the cells giving off small branched fibres (Figs. 87 and 88). The axis-cylinder process of the inferior cornual cell is, excepting in very rare instances, without collaterals (Fig. 88).

The inferior and lateral white columns are composed of fibres which originate from nerve-cells in the grey matter of the cord itself; the fibres in these columns give off collateral fibres which again enter the grey matter, and finally the fibre itself, as we saw in the superior column, bends round and terminates in the grey matter of the cord. It is observed that none of these fibrils are in continuity with nerve cells, nor do the fibrils anastomose among themselves. The inferior and lateral columns of one side of the cord receive fibres from the opposite side, and these, with the aid of the collateral fibres which are returning in the

FIG. 88.—A NERVE-CELL IN THE INFERIOR CORNU OF THE LUMBAR REGION OF AN OX EMBRYO (LANDOIS AND STIRLING, AFTER GOLGI).

n, Axis-cylinder process passing at n' into a longitudinal fibre of the inferior column; n'' much branched lateral process of n.

opposite direction, help to constitute the anterior commissure.

Corresponding to this arrangement of the fibres it is found that three different kinds of nerve cells exist in the grey matter: (1) the large multipolar cell of the inferior cornua in which the motor fibres begin, (2) cells supplying the fibres which pass into the inferior and lateral columns of the cord, and (3) cells found only in the superior cornua, giving off a process which is confined entirely to the grey matter and breaking up in it. In connection with all these cells it is important to bear in mind that the branched processes do not anastomose, although they are often continued for a considerable distance.

The chief features which recent inquiry has brought to light are the collateral branches of fibres; these fibrils do not anastomose, but terminate by surrounding and perhaps coming into contact with nerve cells. This latter fact would go to show that many of the impulses conveyed to the cord can only act on the nerve cells by contact without continuity.

Function of Spinal Nerves.—If the superior spinal roots be divided all parts supplied by them below the division lose sensation, but if the portion of nerve in connection with the spinal cord be irritated pain is produced. If the inferior roots be divided all parts supplied by the nerves below the seat of division suffer motor paralysis; if the cut end of the nerve still in connection with the tissues be irritated the muscles contract vigorously, while if the piece of nerve in connection with the cord be irritated nothing happens. In this way it is demonstrated that the sensory impulses pass into, whilst the motor impulses pass out of the cord. Sometimes pain is felt when the motor roots are divided, due to one or two branches of the sensory nerves finding their way in to the cord by this channel; the phenomenon is known as *recurrent sensibility.*

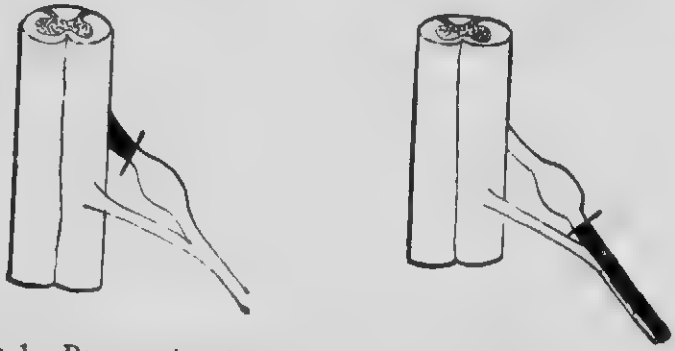
The function of the inferior or motor roots is to supply all the voluntary muscles with the power of movement, the bladder, uterus, intestines, and other hollow viscera and the bloodvessels, with the power to contract and dilate, secretory fibres to the sweat-glands of the skin, and perhaps 'nutritive' nerves to the tissues. Many of the nerve fibres of the efferent or inferior roots are distributed *via* the sympathetic system; from which nerve cells in the cord they arise is not at present known, but after leaving the cord in the inferior roots they join the vertebral ganglia of the sympathetic under the name of the 'rami communicantes' of those ganglia, thus establishing a communication between these two important systems (see p. 394).

The spinal sensory fibres endow the whole of the body with sensation, with the exception of certain parts of the face.

Wallerian Degeneration.—As the result of dividing the spinal nerves degeneration of these occurs; if the superior root be divided *above the ganglion* degeneration occurs upwards into the spinal cord, and there affects certain bundles of fibres, which are really the fibres of the superior roots continued into the spinal cord, and running especially forward towards the head (Fig. 89—1). If the root be divided *below the ganglion* the degeneration takes place in a downward direction, involving the whole length of the nerve below the ganglion (Fig. 89—2); if the trunk be divided both above and below the ganglion degeneration above and below occurs, but the ganglion remains unaffected. If the entire nerve be divided below the ganglion, both the efferent and afferent fibres of which it is composed degenerate below the section (Fig. 89—3).

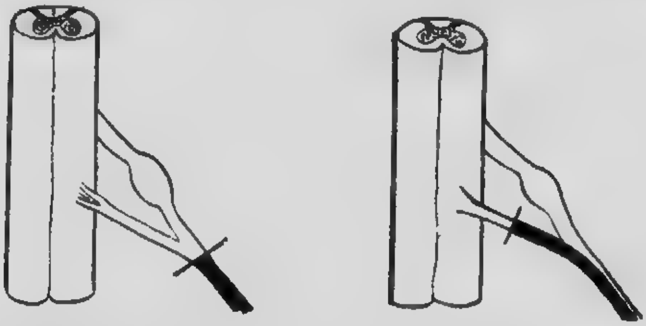
All this is explained by saying that the ganglion is the seat of nutrition of the sensory nerve-fibres, and whichever part of the superior root is cut off from its nutritive influence degenerates; or in other words, the ganglion contains the nerve cells, of which the sensory nerve fibres of the nerve are the axis-cylinder processes.

If the inferior nerve roots be divided degeneration of these also occurs, but the degeneration extends *down* the trunk of the nerve, and does not run up into the spinal cord (Fig. 89—4), the explanation being that the seat of nutrition of the motor nerves lies in the spinal cord, so that degeneration occurs below the cut part and not above it. Their nutrient centre is the multipolar ganglion cell in the inferior cornu of the grey matter of the cord.



No. 1.—Degeneration of afferent fibres caused by a section of superior root above the ganglion.

No. 2.—Degeneration of afferent fibres below a section of superior root below the ganglion.



No. 3.—Degeneration of efferent and afferent fibres below a section of the entire nerve.

No. 4.—Degeneration of efferent fibres below a section of inferior root.

FIG. 89.—DIAGRAMS TO ILLUSTRATE WALLERIAN DEGENERATION OF NERVE ROOTS (WALLER).

These degenerative changes were first described by Waller, and the means they supply of tracing out the tracts of fibres in the central nervous system is hence known as the Wallerian method.

Tracts in the Cord.—The white matter of the cord can be mapped out into columns or tracts, which are quite distinct from the columns into which the cord is anatomically divided. Some of these tracts convey impulses from the cord to the brain, and are known as ascending tracts; others convey impulses from the brain to the cord, and are known as descending tracts.* These ascending and descending tracts have not been made out by ordinary observation, but by experimental inquiry and embryological studies. It was found that after division of certain nerves, or injuries to certain parts of the brain or spinal cord, particular

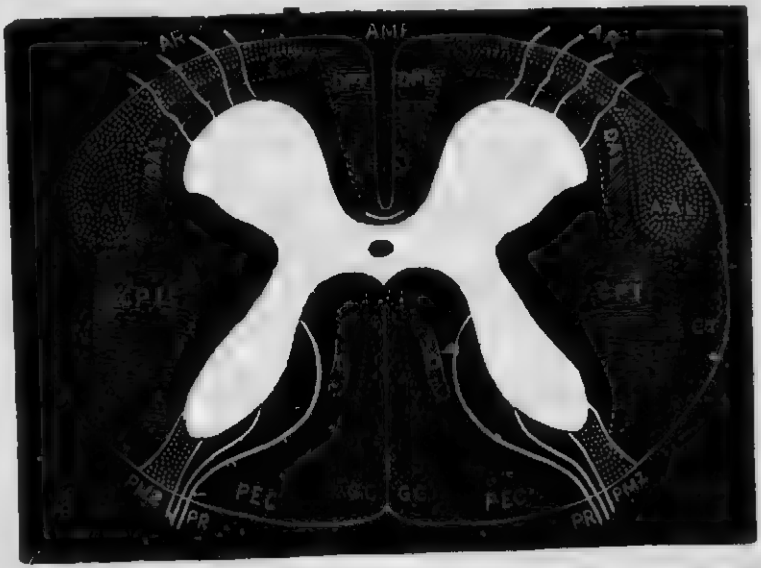


Fig. 90.—Scheme showing the Degeneration Tracts, and the Paths which do not undergo Degeneration in the Cord (Landois and Stirling).

AMF, Inferior median fissure; DPT and CPT, direct and crossed pyramidal tracts. AR, inferior root; PR, superior root of spinal nerves; AAL and DAL, ascending and descending infero-lateral tracts; CT, cerebellar tract; GC, column of Goll; D, comma-shaped tract; PMZ, superior marginal zone; PEC, posterior-external column. The parts left black do not undergo degeneration; the ascending degenerations are shaded with dots, the descending with lines.

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* We have hesitated to adopt the terms ascending and descending, as not harmonizing with the terms employed in dealing anatomically with the cord of the quadruped, but it is difficult to find a suitable substitute.

tracts became degenerated either in a forward or backward direction. By this and other means, it was ascertained that certain paths or tracts exist in the white matter of the cord, connecting the brain with the cord and *vice versa*. It must not be supposed that the function of an ascending or descending tract is necessarily entirely exerted in the direction given to it by its name; the tracts are called ascending or descending according to the direction taken by the degeneration.

The following are the main tracts in the cord (see Fig. 90):

Descending Tracts.	*Ascending Tracts.*
Crossed pyramidal tract.	Direct cerebellar tract.
Direct pyramidal tract—column of Türck (only found in man and anthropoid apes).	Median superior tract—column of Goll.
Infero-lateral descending tract.	Lateral superior tract—column of Burdach.
	Infero-lateral ascending tract.

These paths, known to various observers by somewhat different names, are distributed between the superior, lateral, and inferior columns. The tracts are not found throughout the entire length of the cord, and those descending diminish in size from the head to the tail, those ascending diminish from tail to head.

The *crossed pyramidal tract* is large in man but small in the dog (Fig. 91); it is in connection with the motor region of the brain, and its great size in man appears to bear a distinct relation to the development of the motor region of the cerebrum. The fibres which form it arise in the motor areas of the cerebrum and find their way to the bulb (medulla), where they cross at the pyramids to the opposite side of the cord, and descend in a region external to the superior cornu.

The *infero-lateral descending tract* arises from the mid-brain: it travels down the same side of the cord.

The *direct cerebellar tract* arises from the cells of Clarke's column; the fibres composing it are very large and run headward to end in the cerebellum.

The *median superior tract* occupies a position on the superior part of the cord on either side of the median fissure; it is a sensory tract and is affected in locomotor ataxia of the human subject. The fibres composing it are small and the tract terminates at the bulb;* degeneration of this tract follows division of the superior spinal roots, and the fibres composing it have their trophic centre in the ganglion of these roots, being cell processes from the cells of the ganglion.

The *lateral superior tract* is made up of the fibres of the sensory roots; some of these fibres plunge into the grey matter at once and end there, others pass in the preceding tract, the median superior, and run for a great distance forward, many even reaching the bulb.

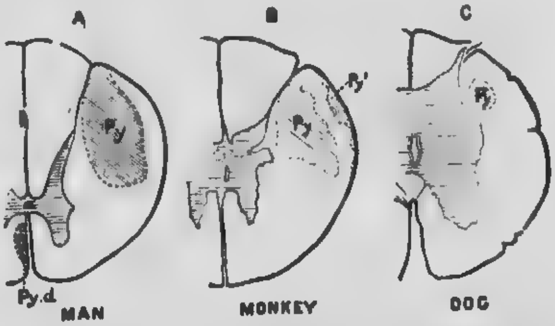

Fig. 91.—Diagram to illustrate the Relative Size of the Crossed Pyramidal Tract (Py) in the Dog, Monkey, Man (Foster, after Sherrington).

In B, Py' is an outlying portion of the pyramidal tract separated from the rest by the cerebellar tract. Py.d in A is the direct pyramidal tract only present in man.

The *infero-lateral ascending tract* runs the entire length of the surface of the cord; the origin of it is not clearly known; degeneration cannot be brought about by dividing the superior roots, so that its origin must be in the cord. It runs headward to terminate in the cerebellum.

It has not been found possible to divide the whole of the white matter into tracts; even after all the above have been defined, there is still much left unaccounted for.

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* The word 'bulb' is used throughout to indicate the medulla oblongata.

When the various tracts in the spinal cord reach the bulb they undergo change in form, position, and distribution, in order that they may arrive at the various parts of the brain to which they are proceeding. Some tracts, however, are known to pass unbroken through the bulb, viz., the pyramidal tract from the cerebrum and the cerebellar tracts; all the others are broken up.

Afferent and Efferent Paths in the Cord.—By experimental inquiry certain paths have been made out in the cord whereby impressions are transmitted from the centre to the periphery and from the periphery to the centre. We have previously spoken of the ascending and descending tracts, as representing the direction in which degenerations travel along given portions of the cord.

By the superior columns of the cord such impressions as temperature, pressure, and muscular sense are conveyed to the cerebrum, running along the same side of the cord by which they entered, and when reaching the bulb crossing over to the opposite side (Fig. 92).

In the lateral columns painful sensations are transmitted, and it is supposed that on entering the cord a large number of the fibres cross over to the opposite side, so that both sides of the cord are transmitting painful impulses. Those fibres which do not decussate in the cord do so in the bulb.

The whole of the afferent fibres entering the cord do not reach the brain, many of them enter the grey matter and terminate by breaking up around cells, and in this way the afferent fibres contract connections with many of the spinal segments in front of it.

In the direct cerebellar tract, impulses believed to be connected with the maintenance of the body equilibrium are transmitted to the brain; the whole of the fibres composing this tract do not reach the cerebellum, some, as just indicated, terminating in the cord itself. All voluntary motor impulses originate in the cerebrum and travel direct to the bulb; here they cross over and run down the opposite side

FIG. 92.—DIAGRAM OF THE AFFERENT AND EFFERENT PATHS PASSING TO AND FROM THE BRAIN BY THE CORD (SHERRINGTON).

L, Left, R, right; CBM, cerebrum; cbm, cerebellum; mo. medulla oblongata containing the decussation of *p*, the pyramidal tract, and of *f*, the fillet; the decussation of *f* should really be a little higher instead of a little lower than that of *p*; *no*, nucleus gracilis (Goll's); *oT*, optic thalamus; *pvc*, the posterior vesicular column, or column of Clarke; *sp g*, spinal ganglion; *co*, median posterior column (Goll's); *dc*, direct cerebellar tract.

The arrows show the direction of the impulses. A centripetal impulse, say from the skin, passes up the afferent nerve, through the spinal ganglion, and enters the superior columns of the cord; it may pass to the cerebrum direct *viâ* the medulla by *co*, the median posterior column, which crosses in the bulb and so gains the opposite side of the brain: or the impulse may pass by *dc*, the cerebellar tract, to the cerebellum, entering it on the same side, and from here crossing over to the opposite cerebral hemisphere. A centrifugal impulse originates in the cerebral cortex, gains the pyramidal tract, passes through the bulb to the *opposite* side of the cord, enters the cells in the inferior cornu of the grey matter, and passes out of this as the inferior spinal nerve.

of the cord, travelling by the crossed pyramidal tract to the multipolar cells of the inferior cornu of the grey matter, from which the motor nerves arise (Fig. 92). These efferent fibres are the longest in the cord, for unlike the afferent fibres they have few connections with spinal segments, and practically run direct from their origin to their termination.

It will be observed that all sensory impulses enter the brain on the side opposite to their origin, whilst all motor impulses leave the brain on the opposite side to that to which they are distributed, so that injury to a motor area of the right brain leads to a left-sided body paralysis.

In the lateral columns of the cord both vaso-motor and sweat nerves travel; decussating in the cord they enter the grey matter of the opposite inferior cornu, and pass out with the motor nerves from the spinal cord.

Reflex Action.—Nerve fibres do not under natural circumstances *generate* impulses, they transmit them but without modifying them; modification can only occur in nerve centres, such as the brain and spinal cord, and these centres always consist largely of nerve-cells, of which the nerve-fibres leaving or entering the centre are simply processes or branches. Dealing at present solely with the spinal cord, it may be described not as one long centre, but a series of centres lying end to end, each capable to a greater or less extent of acting independently of its neighbour, and each centre possessing its afferent and efferent roots.

In these segments of spinal cord, complex acts can be initiated by the arrival of simple centripetal impulses; such acts may be carried out without any assistance from the brain, for they can readily be demonstrated in an animal where the brain has been destroyed. These acts are known by the name of reflex, from which we must not infer that a centripetal impulse is simply reflected into an efferent channel, but rather that a centripetal impulse reaches the cord, and passing into the grey matter stimulates the ganglionic cells which generate the efferent impulse.

The structures necessary for a simple reflex act are (1) an afferent nerve to convey the impression to a nerve centre; (2) a nerve centre in which the outgoing impulses are generated; (3) an efferent channel for their transmission. More complex acts may need more afferent nerves, a larger number of excitable centres, and a greater number of efferent fibres.

A classical example of a reflex act is the drawing up of the leg when the foot is pinched in a frog from which the brain has been entirely removed. Depending upon the degree of pressure applied to the foot, it draws up either one leg or both, *i.e.*, the reflex movements are unilateral or symmetrical, according to the number of ganglionic centres in the cord which have been stimulated. Still greater violence applied to the foot of this brainless frog will affect a larger number of centres further forward in the cord, so that the fore-limbs may share in the reflex, and this is known as *irradiation;* still further excitation may produce convulsive movements of the entire body, known as *general action*.

The brainless frog reacts more regularly to this experiment than one possessing a brain, which is evidence that the brain is capable of exercising a controlling influence or inhibitory effect over reflex actions.

One very prominent feature of a reflex act is its apparently purposeful character; turning once more to the brainless frog, if an acid be applied to the skin of the flank the foot endeavours to remove the source of irritation.

In the dog very characteristic reflex actions occur after division of the cord, such as those of walking, galloping, micturition, and defæcation; tickling the skin causes the animal to scratch the part with the hind foot.

The higher we ascend in the animal scale the less easy is it to obtain evidence of free spinal reflexes—viz., reflexes which take place without any guidance from the brain. This may perhaps be due to a more constant influence exercised over them by the brain. Still, locomotion is often essentially a reflex act, and is very complicated; for instance the tactile and muscular centripetal impulses required, the exact grouping of muscles, and the regulation of the degree and rapidity of contraction, would appear at first sight to need the supervision of the highest centres in the brain, but such is not the case; a pigeon will fly after decapitation. If a horse had to think of every step he had to take he would soon be worn out and blunder. That the higher centres do at times come into play is shown by the judgment which the horse exercises when jumping, viz., the proper distance to take off at, the amount of muscular contraction required to lift the body, and the needful height to which it should be raised, etc., are all evidence of this.

By a **Co-ordinate Movement** is meant one in which the contraction of various related groups of muscles is so adjusted that the extent of their contraction, and everything necessary for a perfect movement, is present and faithfully carried out. This co-ordination of movement we have seen may occur even without the assistance of the brain, and we have alluded to the complex co-ordinate movements of locomotion as an example of this. In the spinal cord, therefore, not only reflex but co-ordinate movements are generated; even the crossed or diagonal movements of locomotion in quadrupeds are of this nature, and are carried out by the spinal cord. Movements which are irregular and purposeless, or in any way fail to co-ordinate, are termed inco-ordinate.

The Stepping Reflex.—As an example of reflex action that of stepping may be considered. When in the dog the spinal cord has been severed in the hinder part of the cervical region and the 'shock' from the transection has passed off, reflex walking is observable. The walking movement includes alternate flexing and straightening of the limb. The forward movement of the hind leg in taking a step is produced by flexion at the hip, and to prevent the foot brushing against the ground as the leg swings forward flexion occurs at the stifle and hock so as to somewhat raise the foot. The limb is then straightened again, so that the foot may reach the ground and bear the weight of the body. In order to prevent the limb doubling up under this burden the extensor muscles which support the patella joint and hock from bending have to contract with sufficient power. Stiffened by the contraction of these muscles the limb serves as a prop to carry the body. While the foot rests on the ground the body moves forward so that in due course the hip advances in front of a vertical drawn upward from the foot. The extended hind limb at this time is sloped somewhat backward as well as downward. When this posture is reached the extensor muscles are thrown into further action, and give the limb a push off from the ground, propelling the body forward. The hind limb thus makes its contribution to the progression forward of the body. In galloping this extensor thrust is very marked, and is given by both hind legs together, instead of alternately as in walking and running.

In this reflex, spinal stepping, we may study first the flexion of the limb which occurs in the forward movement of the step. Flexion similar but more pronounced can be easily excited in the *spinal dog** by exciting the skin of the foot electrically. Though the flexion occurs at hip, patella joint, and hock together, it will be simpler to confine our examination to the flexion at one of these joints only, for what occurs in the muscles of each of the three joints is, so far as concerns us now, the same. The chief muscles which flex the stifle are the *semitendinosus* and *biceps* of the back of the thigh. The electric stimulation of the skin of the foot is found to throw these muscles into contraction, and, with them, also the psoas muscles (flexors of the hip) and the tibialis anticus, etc. (flexors of the hock). But this is only part of what happens. At the same time as the flexors of the stifle contract, the extensor muscles of the stifle, the *vasti* and *crureus*, are relaxed. In order to understand how this comes about it is necessary to refer to a principle of construction of the nervous system which has been termed '*the principle of the common path.*'

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* 'Spinal dog' is the term used for a dog in which the reflexes are entirely spinal, owing to the brain having been destroyed, or the cord having been cut off from the brain.

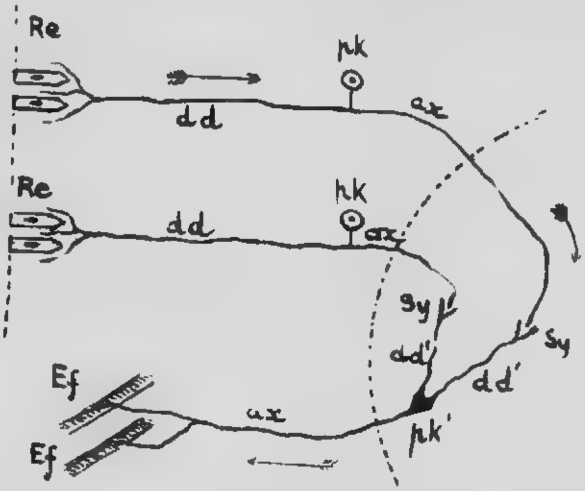

FIG. 93.—DIAGRAM OF A REFLEX ARC (SHERRINGTON).

dd, dd', Dendrites; pk, pk', perikaryon; ax, ax', axones; sy, synapse. dd + pk + ax = neurone; (dd + pk + ax) + sy + (dd' + pk' + ax') = conductor; Re, Re = receptors (epithelial); Ef, Ef = effectors (muscle).

The parts within the dotted line lie in the grey matter of the nerve centre.

The structures along which the nervous impulse in a reflex action runs constitute what is called a *reflex arc.* A reflex arc is a chain of nerve cells (Fig. 93). Each nerve cell consists of three parts: (1) a cell body containing the nucleus and called the *perikaryon*; (2) one or more (usually many) branches from the perikaryon, called *dendrites*, which conduct impulses to the perikaryon; (3) one branch from the perikaryon which conducts impulses away from the perikaryon, and this branch is called the *axone*. The whole nerve cell thus composed of these three parts is termed a *neurone*. The neurones forming a reflex arc follow each other end to end like links in a chain. In the chain the neurones composing it are joined in such a way that the axone of one neurone meets the dendrites of the next neurone, and these junctions of the axone of one neurone with the dendrites of the next are of such a nature that conduction of impulses from one neurone to the next occurs in one direction only, that is from axone to dendrite, and not backwards from dendrite to axone. These junctions between neurones are termed *synapses* (see Fig. 93).

The first link of each reflex chain is a neurone which starts in a receptor organ, *e.g.*, a sense-organ. A receptive field, *e.g.*, an area of skin, is always analysable into receptive points, and the nerve-path of the reflex always starts from a receptive point or points. A single receptive point may play reflexly upon quite a number of different effector organs. It may be connected through its reflex path with many muscles and glands in various parts. Yet all its reflex arcs spring from the one single shank, so to say; that is, from the one afferent neurone that conducts from the receptive point at the periphery into the central nervous organ. This neurone dips at its deep end into the great central nervous organ, the cord or brain. There it enters a vast network of conductive paths. In this network it forms manifold connections. So numerous are its potential connections there that, as shown by the general convulsions induced under strychnine-poisoning, its impulses can discharge practically every muscle and effector organ in the body. Yet under normal circumstances the impulses conducted by it to this central network do not irradiate there in all directions. Though their spread over the conducting network does, as judged by the effects, increase with increase of stimulation of the entrant path, the irradiation remains limited to certain lines. Under weak stimulation of the entrant path these lines are sparse. The conductive network affords, therefore, to any given path entering it some communications that are easier than others. This canalization of the network in certain directions from each entrant point is sometimes expressed, borrowing electrical terminology, by saying that the conductive network from any given point offers less resistance along certain circuits than along others. This recognizes the fact that the conducting paths in the great central organ are arranged in a particular pattern. The pattern of arrangement of the conductive network of the central organ reveals something of the integrative function of the nervous system. It tells us what organs work together in time relationship. The impulses are led to this and that effector organ, gland, or muscle in accordance with the pattern.

At the commencement of every reflex arc is a receptive neurone, extending from the receptive surface to the central nervous organ (see Fig. 93). That neurone forms the sole avenue which impulses generated at its receptive point can use whithersoever may be their distant destination. That neurone is, therefore, a path exclusive to the impulses generated at its own receptive points, and other receptive points than its own cannot employ it.

But at the termination of every reflex arc we find a final neurone, the ultimate conductive link to an effector organ, gland, or muscle. This last link in the chain, *e.g.*, the motor neurone, differs in one important respect from the first link of the chain. It does not subserve exclusively impulses generated at one single receptive source alone, but receives impulses from many receptive sources situate in various regions of the body (see Fig. 93). It is the sole path which all impulses, no matter whence they come, must travel if they would reach the muscle-fibres which it joins. Therefore, while the receptive neurone forms a *private* path exclusively for impulses of one source only, the final or efferent neurone is, so to say, a public path, *common* to impulses arising at any of many sources in a variety of receptive regions of the body. The same effector organ stands in reflex connection not only with many individual receptive points, but even with many various receptive *fields*. Reflex arcs arising in manifold sense-organs can pour their influence into one and the same muscle. A limb-muscle is the *terminus ad quem* of nervous arcs arising not only in the right eye but in the left, not only in the eyes but in the organs of smell and hearing; not only in these, but in the otic labyrinth, in the skin, and in the muscles and joints of the limb itself and of the other limbs as well. Its motor nerve is a path common to all these.

Reflex arcs show therefore the general feature that the initial neurone is a private path exclusive for a single receptive point, and that finally the arcs embouch into a path leading to an effector organ, and that this final path is common to all receptive points wheresoever they may lie in the body, so long as they have any connection at all with the effector organ in question. Before finally converging upon the motor neurone, the arcs usually converge to some degree by their private paths, embouching upon internuncial paths common in various degree to groups of private paths. The terminal path may, to distinguish it from internuncial common paths, be called *the final common path* (see Fig. 93). The motor nerve to a muscle is a collection of such final common paths.

A result is that each receptor being dependent for communication with its effector organ upon a path not exclusively its own but common to it with certain other receptors, that nexus necessitates successive and not simultaneous use of the common path by various receptors using it to different effect.

The Scratch Reflex.—Good opportunity for study of this correlation between reflexes is given in the 'scratch reflex.' When the spinal cord has been transected in the neck, this reflex in a few months becomes prominent. Stimuli applied within a large saddle-shaped field of skin (Fig. 94) excite a scratching movement of the leg. The movement is rhythmic flexion at hip, stifle, and hock. It has a frequency of about four per second. The stimuli provocative of it are mechanical, such as rubbing the skin, or pulling lightly on a hair. The nerve-endings which generate the reflex lie in the surface layer of the skin, about the roots of the hairs. A convenient way of exciting these is by feeble faradization.

Prominent among the muscles active in this reflex are the flexors of the hip. If we record their rhythmic contraction we obtain tracings as in Fig. 96. A series of brief contractions succeed one another at a certain rate, whose frequency is independent of that of the stimulation. The contractions are presumably brief tetani. The stimulus to the hair-bulbs of the shoulder throws into action a lumbar spinal centre, innervating the hip-flexor, much as the bulbar respiratory centre drives the spinal *phrenicus* centre. In the case of the respiratory muscle the frequency of the rhythm is, however, much less.

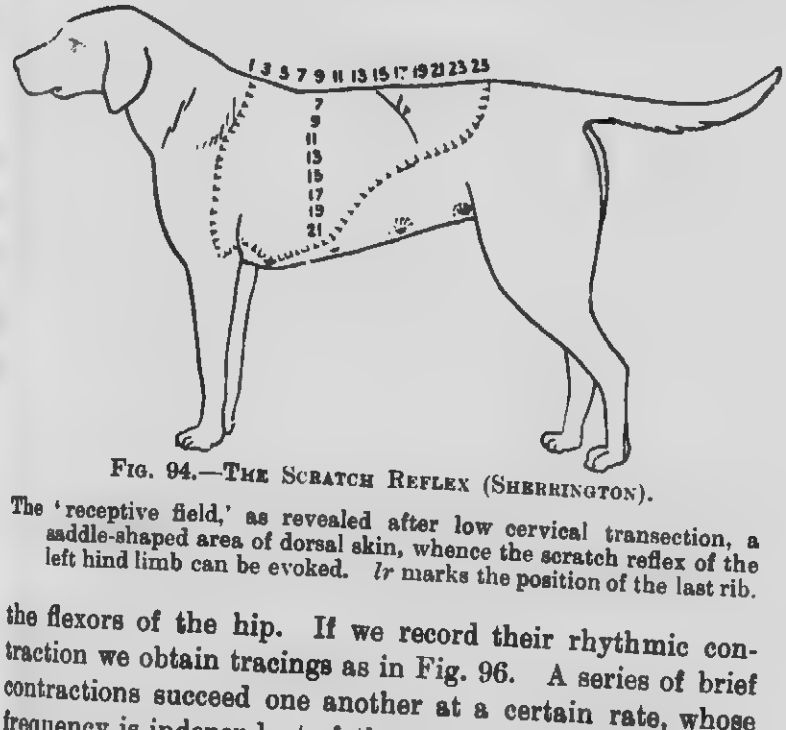

Fig. 94.—The Scratch Reflex (Sherrington).

The 'receptive field,' as revealed after low cervical transection, a saddle-shaped area of dorsal skin, whence the scratch reflex of the left hind limb can be evoked. *lr* marks the position of the last rib.

The reflex is unilateral: stimulation of the left shoulder evokes scratching by the left leg, not by the right. In the lateral column of the spinal cord *long* fibres exist directly connecting the spinal segments of the shoulder with the spinal segments containing the motor neurones for the flexor muscles of the hip, and knee, and ankle. We thus arrive at the following reflex chain for the scratch reflex: (i.) The receptive neurone (Fig. 95, sα), from the skin to the spinal grey matter of the corresponding spinal segment in the shoulder. This is the exclusive or private path of the arc. (ii.) The long descending proprio-spinal neurone (Fig. 95, Pα), from the shoulder segment to the grey matter of leg segments. (iii.) The motor neurone (Fig. 95, FC), from the spinal segment of the leg to the flexor muscles. This last is the *final common path*. The chain thus consists of three neurones. It enters the grey matter twice, that is, it has two neuronic junctions, two synapses. It is a *disynaptic* arc.

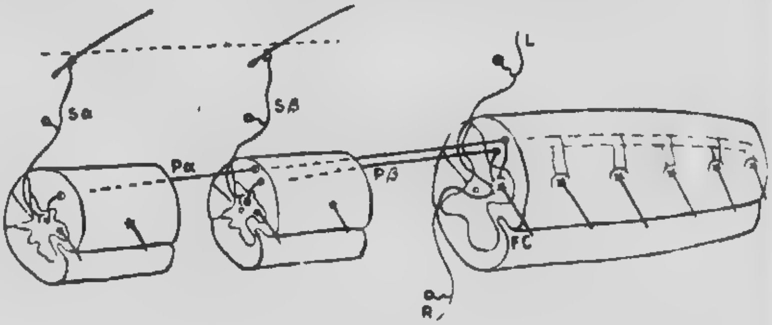

FIG. 95.—SPINAL ARCS INVOLVED IN SCRATCH REFLEX (SHERRINGTON).

Diagram of the spinal arcs involved in Fig. 94. L, receptive or afferent nerve path from the left foot; R, receptive nerve-path from the opposite foot; sα, sβ, receptive nerve-paths from hairs in the dorsal skin of the left side; FC, the final common path, in this case the motor neurone to a flexor muscle of the hip; Pα, Pβ, proprio-spinal neurones.

Now if, while stimulation of the skin of the shoulder is evoking the scratch reflex, the skin of the hind foot is stimulated, the scratching is arrested. Stimulation of the skin of the hind foot causes the leg to be flexed, drawing the foot up. The drawing up of the foot is effected by strong tonic contraction of the flexors of hock, stifle, and hip. In this reaction the reflex arc is (i.) the receptive neurone (Fig. 95, L) (nociceptive) from the foot to the spinal segment; (ii.) perhaps a short intraspinal neurone; and (iii.) the motor neurone (Fig. 95, FC) to the flexor muscle, *e.g.*, of hip. Here, therefore, we have an arc which embouches into the same *final common path* as *sa*. The motor neurone FC is a path common to it and to the scratch reflex arcs; both arcs employ the same effector organ, a hip flexor.

The channels for both reflexes finally embouch upon the same common path. The flexor effect specific to each differs strikingly in the two cases. In the scratch-reflex the flexor effect is an intermittent contraction of the muscle; in the foot-reflex it is steady and maintained. The accompanying tracing (Fig. 96) shows the result of conflict between the two reflexes. The one reflex displaces the other from the common path. There is no compromise. The scratch reflex is set aside by that of the nociceptive arc from the foot. The stimulation which previously sufficed to evoke the scratch reflex is no longer effective, though it is continued all the time. But when the stimulation of the foot is discontinued the scratch reflex returns. In that respect, although there is no enforced inactivity, there is inhibition. There is interference between the two reflexes, and the one is inhibited by the other. Though there is no cessation of activity in the motor neurone, one form of activity that was being impressed upon it is cut out and another takes its place.

Suppose, again, during the scratch reflex, stimuli are applied to the foot, not of the scratching but of the opposite side (Fig. 95, R). This stimulation of the foot causes flexion of its own leg and extension of the opposite. If, when the left leg is executing the scratch reflex, the right foot is stimulated, the scratching, involving as it does the left leg's flexors, is cut short. This inhibition of the flexor scratching movement occurs sometimes when the con-

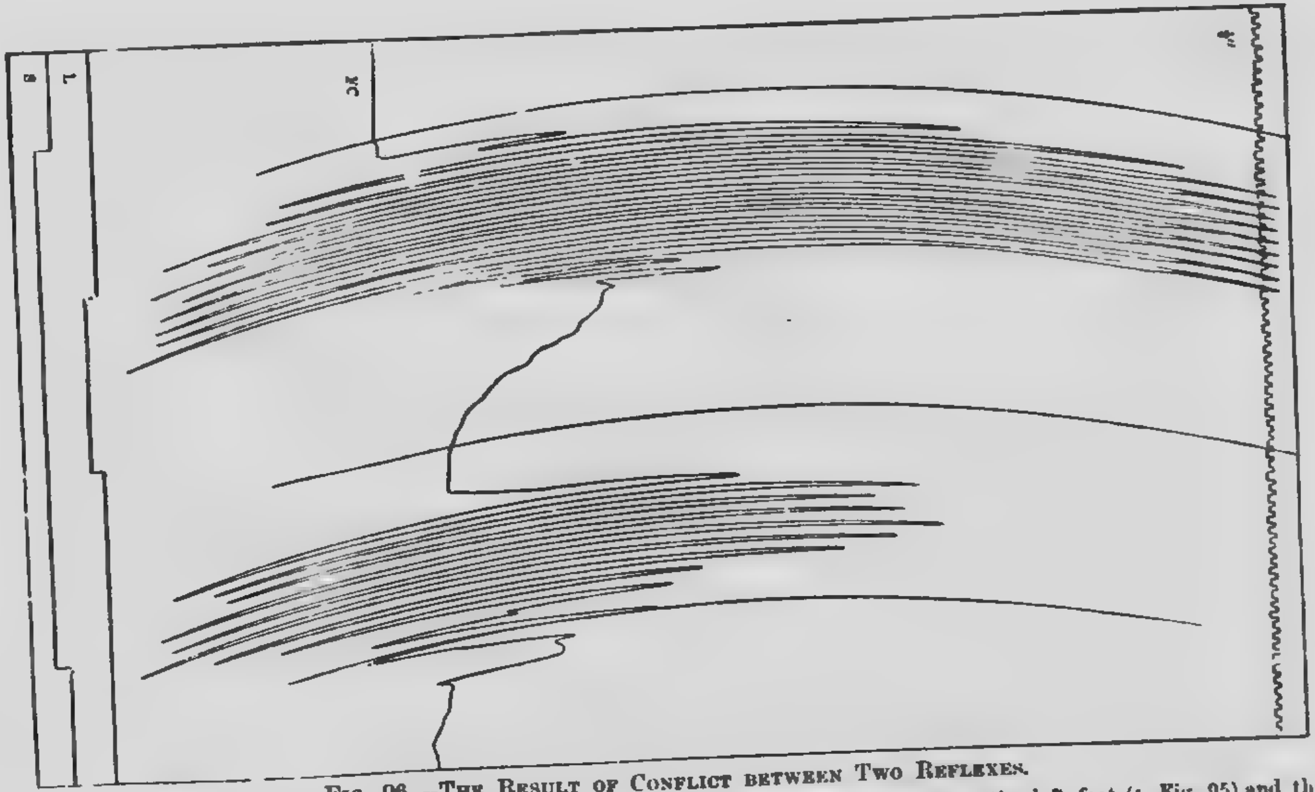

FIG. 96.—THE RESULT OF CONFLICT BETWEEN TWO REFLEXES.

Interference between the reflex action of the left hip flexor, FC, caused by the nervous arc from the left foot (1, Fig. 95) and the scratch reflex. The stimulation of the dorsal skin (Fig. 95) inducing the scratch-reflex began at the beginning of the notch in the signal line S, and continued throughout the period of that notch. Later, for the period marked by the notch in signal line L the stimulation of the foot was made. This latter stimulation interrupts the clonic scratch reflex in the manner shown. The time is registered above in fifths of seconds. The tracing reads from left to right. It is noteworthy that the interruption of the scratch reflex by the foot reflex is not established directly the foot stimulus begins, and that it [illegible] for a short time the application of the foot stimulus.

traction of the extensors is minimal or hardly perceptible.

It is obvious from this that the final common path, FC, to the flexor muscle can be controlled by, in addition to the before-mentioned arcs, others that actuate the extensor muscles, for it can be thrown out of action by them. The final path, FC, is therefore common to the reflex arcs, not only from the same side foot (Fig. 95, L) and shoulder skin (Fig. 95, sα, sβ), but also to arcs from the opposite foot (Fig. 95, R), in the sense that it is in the grasp of all of them. In this last case we have a conflict for the mastery of a common path, not, as in the previous instance, between two arcs, both of which use the path in a pressor manner although differently, but between two arcs that, though both of them control the path, control it differently, one in a pressor manner heightening its activity, the other in a depressor manner lowering or suppressing its activity.

We said that the scratch reflex is unilateral. If the right shoulder be stimulated, the right hind-leg scratches; if the left shoulder be stimulated, the left hind-leg scratches. If both shoulders be stimulated at the same time, one or the other leg scratches, but not the two together. The one reflex that takes place prevents the occurrence of the other. The reason is, that although the scratch reflex appears unilateral, it is not strictly so. Suppose the left shoulder stimulated. The left leg then scratches. If the right leg is then examined it is found to present slight, steady extension with some abduction. This extension of the leg which accompanies the scratching movement of the opposite leg contributes to support the animal on three legs, while it scratches with the fourth.

Suppose now we stimulate the left shoulder, evoking the scratching movement of the left leg, and that the right shoulder is at the same time appropriately and strongly stimulated. This latter stimulus often inhibits the scratching movement in the opposite leg and starts it in its own. In other words, the stimulus at the right shoulder not only sets the flexor muscles of the leg of its own side into scratching action, but it inhibits the flexor muscles of the opposite leg. It throws into contraction the extensor muscles of that leg. In the previous example there was a similar co-ordination. The motor nerve to the flexor muscle is therefore under the control not only of the arcs of the scratch reflex from the homonymous shoulder, but of those from the crossed shoulder as well. But in regard to their influence upon this final common path, the arcs from the homonymous shoulder and the opposite shoulder are opposed.

Experiments show that this inhibition does not take place in the motor nerve itself. Many circumstances connect it with the place where the converging neurones come together in the grey matter at the commencement of the common path. The field of competition between the rival arcs seems to lie in the grey matter, where they impinge together upon the final or motor neurone. That is equivalent to saying that the essential seat of the phenomenon is the synapse between the motor neurone and the axone-terminals of the penultimate neurones that converge upon it. There some of these arcs drive the final path into one kind of action, others drive it into a different kind of action, and others again preclude it from being activated by the rest.

We are now in a position to return to the flexion at the stifle in the reflex act of stepping. We see that the same stimulus which excites the motor neurones of the flexors to discharge motor impulses into those muscles, causes the motor neurones of the antagonistic muscles, the extensors of the knee, to cease discharging impulses, and keeps them prevented from discharging impulses. The stimulus sets up an intraspinal *excitation* of the motor neurones of the flexor muscles and an *intraspinal inhibition* of the motor neurones innervating the extensor muscles.

When the flexion phase of the act of stepping has been passed through, the leg extends again, perhaps by its own weight, perhaps by return of activity in the motor neurones of the extensor muscles which had been inhibited. In due course the foot reaches the ground. When it does so the weight of the body gradually comes upon it, and soon presses the sole of the foot with its full force against the ground. A stimulus is thus given to nerve-endings in the sole. This stimulus can be imitated; for instance, by pressing against the sole of the foot with a finger. This, in the spinal dog, even when the animal is lying on its side, excites a strong reflex extension of the limb, the 'extensor thrust.' Just such an extension occurs when the foot is pressed against the ground by the weight of the body in the act of stepping. This extensor thrust gives the propulsive movement of the body forward, which is the contribution made by the limb in its reflex step toward the progression of the animal. The extensor thrust is particularly marked in the gallop, and is then given by the two hind-limbs together, and not alternately, as in walking and running.

The above comparatively simple acts form certainly only a part of the whole complex reflex which really occurs in stepping. In such complex reflexes many stimuli are at work together, and co-operate harmoniously for a co-ordinate result. In walking, running, etc., probably very important sources of the reflex lie in the muscles and joints of proximal parts of the limb—namely, in the joints of the hip and stifle and the great muscles acting on those joints. These joints and muscles are liberally supplied with afferent nerves conducting centripetal impulses from them. The importance of these as sources of the reflex of stepping is indicated by several facts. In the first place, a dog or cat is found still to walk well when all the nerves of all four of the feet have been severed—not only the skin-nerves of the feet, but all their deep nerves as well. In the second place, when the spinal dog is lifted so that its limbs do not touch any solid support whatever, reflex walking and galloping are performed, although the limbs are stepping wholly in the air. But, for this reflex walking in the air, it is necessary that the limbs hang down. The reflex ceases if the dog be inverted, so that gravity no longer is acting on the joints and muscles as it does in the position usually accompanying acts of stepping. Further, it is probable that the spinal centres which execute reflex walking, running, etc., receive much help and direction from afferent arcs which arise in the labyrinth of the ear.

The stimuli, which are the source of reflex walking, etc., arise, therefore, almost certainly in many receptive organs. Individually the action of each of these may be quite weak. They sum up their effect, because their impulses converge on the same final common paths, the motor neurones. The summation is probably largely the work of these motor neurones. Their shape bespeaks for them the function of an organ for such summation. In each motor neurone its dendrites converge to the perikaryon as a meeting place, and there the impulses carried to it by the dendrites add their excitatory effects together. As the synapses are places where inhibition and irreversibility of conduction are established in the reflex arc and where reflex arcs meet, so the perikaryon seems a place where summation of impulses from various harmonious sources are added together for a conjoint effect.

But the reflex acts carried out by the cord are not limited to those affecting skeletal muscles; the act may be a secretory or nutritive one, or involving the contraction or relaxation of pale muscle: for example, the contraction and dilatation of the bloodvessels under the influence of the vaso-motor system, the peristaltic movements of the intestines, the contraction of the bladder and uterus, and the secretions from the various abdominal glands, are all examples of reflex acts. The time occupied by a reflex act varies dependently upon the strength of the stimulus and the nature of the reflex; the sharper the stimulus the more rapid the reflex, the more active the centre the more rapid the response; impulses which have to cross the cord take longer than those which enter and return from the same side. It is mainly during this appreciable delay, as measured by delicate apparatus, that the changes are occurring in the grey substance which lead to an efferent response. In the dog the time occupied by a reflex on the same side is estimated at ·022 up to 2-3 seconds, according to circumstances.

Tendon Reflexes.—The muscle and tendon reflexes, [illegible] well known in the human subject, have not, so far as [illegible] are aware, been studied in the ungulates; nor do we know whether the existence of any reflexes has been demonstrated, if, perhaps, we except the immediate lifting of the foot, which generally follows pressure on the so-called 'chestnut' found on the inside of the fore-arm of the horse.

One of the best known of the tendon-reflexes in man is the knee-jerk, a jerking forward of the leg when the straight ligament of the patella is struck. This is caused by a momentary single spasm of the extensor muscles of the knee, and although often called a reflex act cannot truly be so, because the time between the blow and the jerk is too short for any reflex act. It is well seen in the dog, cat, rabbit, etc. Although not a reflex action it is dependent on the reflex tonus that is maintained in the muscles by the spinal arcs connected with them; if that tonus be much lowered, as by severance of the nervous reflex arc, the jerk can no longer be elicited. The jerk is a good index of the condition of the reflex arc, and therefore of the condition of the activity or depression of the segments of the cord by which the extensor muscles are innervated. It is depressed during sleep or anæsthesia, and by anæmia of the cord; it is intensified when the cerebral restraint is removed from the lumbar spinal segments by diversion or attention to another part, or by severance of the cord in the dorsal region. Another brisk 'jerk' in the dog is the ischial, obtained from the hamstring muscles by tapping the tuberosity of the ischium.

Automatic Action.—Nerve centres are not as a rule capable of issuing impulses which are not the result of an afferent stimulus; one centre there is however which seems to do so. This is the respiratory centre in the bulb (p. 109). In the same way the tone of the vascular system, or the force which keeps the muscular wall of the vessel in the necessary condition of constriction, is in part brought about by automatic impulses. The tone of the muscular walls of the vascular system seems to be due to tonic (permanent) actions, either of local nerve apparatus in the sympathetic system or of the muscular coat itself.

Special Centres in the Spinal Cord.—In the cord certain centres exist, which though ordinarily under the control of a chief centre in the bulb, yet are capable of carrying on peculiar reflex actions even after the cord has been divided, and thus separated from the controlling influence of the bulb.

The *cilio-spinal centre* lies between the cervical and dorsal portions of the cord; in it fibres originate which through the cervical sympathetic supply the dilator muscle of the iris. Destruction of the region in question causes a contraction of the pupil, whilst irritation of it causes the pupil to dilate.

The *ano-spinal* centre, found in the lumbar portion of the cord, controls the act of defæcation; it would appear to be highly developed in herbivora, which possess the power of bringing it into play not only when the body is at rest but during movement. The functions of the ano-spinal centre are rather complex, inasmuch as it has not only to maintain the tone of the sphincter, but also to relax it during defæcation, and under the latter condition simultaneously contracts both the wall of the intestine and the abdominal muscles.

The *vesico-spinal* centre also exists in the lumbar portion of the cord, and governs micturition; its action is similar to that of the ano-spinal centre.

In the lumbar portion of the cord other centres are found, for example, the *erection* centre, the *genito-spinal* centre which contains the nervous apparatus employed in the emission of semen, and the *parturition* centre.

Vaso-motor centres are found throughout the cord; they are principally under the control of similar centres in the bulb, but may act independently. *Sweat* centres are probably closely connected with the vaso-motor centres. *Trophic* centres for the nutrition of the tissues also exist in the cord; destruction of parts by ulceration, or great muscular wasting, may follow injury of the trophic nerves.

The Functions of the Spinal Cord may be summarized as follows: The cord is the central seat of numerous reflex actions; some of these are intermittent and occasional, others permanent or tonic, such as the maintenance of muscular and arterial tone. There is evidence that it assists in co-ordinating movement, and it is also the path by which the brain and the body are brought into connection, both in an upward and downward direction and from side to side.

Cranial Nerves.

These are divided into nerves of special sense, sensory nerves, motor nerves, and mixed nerves. Altogether they make twelve pairs, and all but Nos. 1, 2 and 3 arise from the medulla.

For nerves Nos. 1 and 2 see Smell and Vision, Chapter XV.

Third Pair, or Motor Oculi, is one of the motor nerves of the eyeball; it supplies with motor power all the muscles (excepting the *external rectus* and the *superior oblique*), also the muscle of the upper lid. Through its connection with the lenticular ganglion it supplies fibres to the iris and ciliary muscle; it is also connected at its origin with two other motor nerves of the eyeball, viz., the fourth and sixth pairs.

The deep-seated origin of the third pair is from the corpora quadrigemina and peduncles of the cerebrum. Division of the nerve causes the eye to turn downwards and outwards, owing to the unbalanced action of the superior oblique and external rectus; there is also depression of the upper lip, immobility of the eyeball, and dilatation of the pupil. The action of the third pair will be discussed again in connection with the physiology of sight.

Fourth Pair, or Pathetic.—The motor nerve of the superior oblique muscle of the eyeball; it has a deep-seated origin in the valve of Vieussens.

Fifth Pair, or Pars Trigemini, resembles a spinal nerve in having two roots, a motor and sensory; and the resemblance is carried still further by the sensory root having a large ganglion on it, the Gasserian. The motor root arises from the trigeminal nucleus of the medulla, and is connected with the cerebral cortex on the opposite side. The sensory fibres arise from the sensory trigeminal nucleus, and can be traced downwards into the grey matter of the cord. This nerve also has connections with the nerves arising from the medulla; in this way can be explained the extensive connections and varied reflex acts of the fifth pair.

There are three divisions of the fifth pair of nerves, viz., the ophthalmic, the superior maxillary division, and the inferior maxillary division.

The *ophthalmic* division is the smallest of the three furnished by the Gasserian ganglion; it is exclusively sensory, supplying with sensation the structures over the brow, the eyeball, the lachrymal gland, membrana nictitans, and the pituitary membrane on both sides. The *superior maxillary* division is wholly sensory and supplies part of the orbit, eyelids, skin, hard and soft palates, pituitary membrane of the nostrils, and teeth (molars, incisors, and canine), whilst the terminations of the main trunk are extended over the face, upper lip, and nostrils, by means of a considerable plexus of nerves which issues from the infra-orbital foramen. The *inferior maxillary* division is a mixed nerve; it supplies motor power to the muscles of mastication, viz., the masseters, buccal muscles, internal pterygoid, part of the temporalis, and the mylo-hyoid muscle of the tongue. By means of its great lingual branch, which enters the tongue in conjunction with the chorda tympani of the seventh nerve, common sensation is supplied to the anterior two-thirds of the tongue.

Besides the above, sensory branches are supplied to the teeth and lips near the commissures, and filaments to the parotid, molar, and buccal glands.

Each of these main divisions of the fifth nerve possesses a ganglion on it, viz., the ophthalmic on the ophthalmic branch, the spheno-palatine on the superior branch, and the otic ganglion on the inferior branch. All these ganglia receive branches of nerve from the sympathetic and cerebro-spinal system. It is from the ophthalmic or ciliary ganglion that the ciliary nerves of the iris and ciliary muscle arise, the motor root of the ganglion being supplied by the third nerve, and the sensory from a branch of the ophthalmic of the fifth. The ganglion on the superior branch is known as the spheno-palatine; it receives its motor supply through the Vidian nerve from the facial, its sensory roots being numerous and supplied by the spheno-palatine branch of the fifth. This ganglion supplies branches to the bloodvessels of the orbit, and others to the palate through which motor power is supplied to the muscles of the soft palate. On the inferior division of the fifth is sometimes found a ganglion known as the otic, the motor root of which is derived from the seventh pair, and the sensory from the inferior branch of the fifth. This ganglion gives branches which supply the tensor tympani of the internal ear, and some branches to the Eustachian tube and tensor palati.

In the dog and cat is found the submaxillary ganglion; it is supplied by the chorda tympani of the seventh pair with secretory fibres for the gland and dilator fibres for the bloodvessels; to this ganglion also runs a branch of the sympathetic. All the fibres of the chorda do not enter the gland, some supply the tongue. A submaxillary ganglion exists in both dog and cat; it lies in the hilum of the gland of the same name.

Division of the superior maxillary division of the fifth in the horse (Bell's experiment) prevents the animal from grasping food with its lips; not for the reason that they are deprived of motion, but owing to loss of sensibility the animal is unaware of how to take hold of the food. The relation of the fifth to muscular movements is that it keeps the muscles aware of the position of objects.

Complete section of the fifth pair causes loss of sensation to one side of the face, lips, mouth, and temple, part of the ear, cornea, conjunctiva, nasal mucous membrane, and anterior two-thirds of the tongue. There is paralysis of the muscles of mastication, and the mouth becomes injured by the teeth owing to loss of sensibility; the food collects on the paralyzed side, where it decomposes and produces local irritation. The animal also frequently bites its tongue, as its position in the mouth cannot be felt. The cornea may become cloudy and ulcerates.

As an afferent nerve in reflex acts, the fifth nerve is most important; without it there would be no closure of the eye nor sneezing, and irritation of the conjunctiva would produce no tears.

Sixth Pair, or Abducens, arises from the floor of the fourth ventricle, and supplies the external rectus muscle of the eye with motor power. Paralysis of this muscle causes internal squint.

Seventh Pair (Portio Dura), or **Facial.**—Arises from the medulla, passes through the internal auditory meatus in company with the eighth pair, which it leaves behind in the internal ear, whilst the seventh nerve escapes by the aqueduct of Fallopius, passes beneath the parotid, and finds its way on to the cheek over the external masseter muscle, and is eventually distributed to the upper and lower lips and the alæ of the nostrils. It essentially supplies the muscles of expression and not those of mastication.

In its course it is joined by branches from the fifth pair and vagus, and gives off to the lingual of the fifth, as previously mentioned, a branch known as the chorda tympani, supplying the front portion of the tongue with taste, and secretory fibres to the maxillary gland and dilator fibres to the bloodvessels. It is really a branch not of the facial but of the *nervus intermedius*, the little cranial nerve lying between the facial and the nerve of the ear.

The facial is a motor nerve to the muscles of the middle ear, external ear, cheeks, lips, nostrils, and orbicular muscle of the eye.

Division of the seventh nerve leads to alterations in sight, taste, hearing, smell, and facial expression. As it supplies the muscle which closes the eyelids (the orbicularis palpebrarum), conjunctivitis occurs from exposure of the eyeball; hearing is affected owing to paralysis of the muscles of the internal ear; smell is impaired due to the paralyzed condition of the nostrils; taste is affected through paralysis of the chorda. The expression of unilateral facial paralysis in the horse is characteristic; the upper lip drawn to one side, the elongated nostril, the pendulous lower lip, the escape of saliva and food from the mouth, the vacant look, the open eye, and the drooping ear, point clearly to the extensive distribution of this nerve.

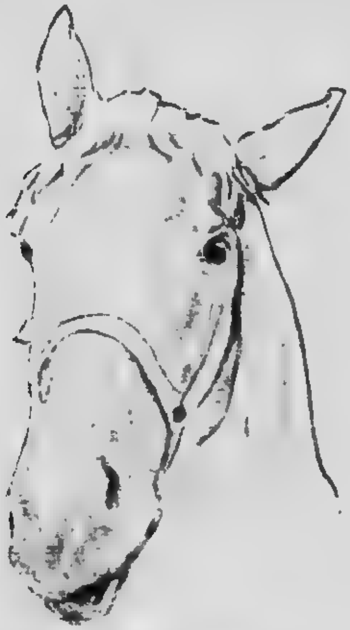

Fig. 97.—Characteristic Facial Expression of the Horse with Paralysis of the Seventh Nerve.

Bernard pointed out that horses were suffocated if galloped after division of both facial nerves, owing to the fact that the nostrils were no longer capable of dilatation.

Eighth Pair, or Portio Mollis.—Arises by two roots, one the nerve for the special sense of hearing, the other distributed to the otolith organs and the semicircular canals, and assists through these in maintaining the equilibrium of the body. Injury to the semicircular canals produces giddiness, not deafness, and certain movements (termed 'pendulum-like') of the head occur; the direction in which these are made depends on the orientation of the canal which has been injured.

Ninth Pair, or Glosso-Pharyngeal, arises from the medulla: it is a mixed nerve, and supplies motor power to the muscles of the pharynx, and sensory fibres to the posterior third of the tongue, soft palate, part of pharynx, and anterior surface of the epiglottis. It is also a special nerve of taste, supplying the posterior third of the tongue, and having special nerve endings, known as 'taste-bulbs,' in the circumvallate papillæ.

Tenth Pair, or Pneumogastric.—This is both a sensory and motor nerve. At its origin in the medulla it is intimately mixed up with the ninth, eleventh, and twelfth pairs of nerves, and later on with the sympathetic. It is the most extensively distributed nerve in the body, supplying the œsophagus, pharynx, lungs, bronchi, trachea, heart, stomach, and intestines; hence its other name, vagus.

The sensory branches of the nerve are not highly endowed with sensation, probably for the reason that their chief function as sensory nerves is as afferent channels for reflex action. The motor fibres are derived from the spinal accessory nerve. In the foramen lacerum the vagus is joined by the jugular ganglion, and for a very short distance it is intimately connected with the accessory nerve; here it receives filaments from the accessory, sympathetic, hypoglossal, and two first cervical nerves. The vagus now descends behind the guttural pouch and joins the cervical portion of the sympathetic nerve, from which results, in the horse and most other animals, a single cord which passes down the neck above the carotid artery; as it enters the chest it separates from the sympathetic. The arrangement of the right and left nerves is different; the right gives off the right recurrent which passes around the dorso-cervical artery, while the main trunk terminates above the origin of the bronchi; the left gives off its recurrent branch opposite to the aorta, and also terminates on the bronchi, forming with the right nerve the bronchial plexus and œsophageal nerves, the latter passing to the stomach and from thence to the solar plexus. The various branches of the vagus may best be studied in the order in which they are given off.

The *pharyngeal nerve* originates at the superior cervical ganglion and passes to the pharynx, where it forms with the ninth pair the pharyngeal plexus. It is a mixed nerve, and supplies the middle and constrictor muscles of the pharynx and the cervical portion of the œsophagus with motor power.

The *superior laryngeal* nerve supplies the mucous membrane of the larynx with remarkable sensibility, and gives a motor branch, the external laryngeal, to the crico-pharyngeus. In most animals the superior laryngeal supplies the crico-thyroid muscle of the larynx with motor power, but in the horse this is supplied by the first cervical nerve. It is the superior laryngeal nerve which reflexly excites coughing, the coughing centre being situated in the medulla; further, it contains afferent fibres in connection with the respiratory centre, which when stimulated cause arrest of respiration: they are therefore inhibitory fibres. Section of the superior laryngeal causes pain, and produces in dogs a deeper and hoarser voice due to paralysis of the crico-thyroid muscle, which can no longer render the vocal cords tense. The absence of sensibility in the larynx allows food to pass into the trachea, and thus produces pneumonia.

The *inferior laryngeal*, or *recurrent*, is given off from the main trunk within the chest, on the left side winding around the aorta from without inwards, and on the right side passing around the dorso-cervical artery; both branches return up the neck and supply all the muscles of the larynx (excepting the crico-thyroid) with motor power. The recurrents are of great practical interest, as they are affected (especially the left) in that common form of disease in the horse known as 'roaring,' which is generally due to paralysis and atrophy of the muscles which dilate the laryngeal opening (see p. 126) After division of both recurrent nerves death by asphyxia is likely to follow. We have however observed complete bilateral paralysis of the larynx in horses without asphyxia being produced. In such cases it has been shown that the age of the horse is the saving factor, the rigidity of the cartilages preventing the arytenoids from completely collapsing over the opening of the glottis.

Division of the recurrent also leads to a partial loss of voice, and a peculiar cough is produced owing to paralysis of the laryngeal muscles. As the recurrent supplies sensory branches to the tracheal portion of the œsophagus and trachea, division causes loss of sensation in these parts.

It is curious that the recurrent laryngeal should contain motor fibres, not only for the dilator but also the constrictor muscles of the larynx; it has been observed that when this nerve gets out of order, it is the *dilator* muscles which first become paralyzed and later the constrictors (p. 125). Irritation of the peripheral end of the recurrent produces spasm of the larynx. There are certain poisons, such as that contained in *Lathyrus sativus* and others of the Leguminosæ, which appear to have a special action on this nerve, or at any rate on the larynx, spasm of the larynx being one of the earliest symptoms of poisoning.

The cardiac branches of the vagus contain the fibres which exercise a controlling and inhibitory power over the heart (see p. 45). They also contain the depressor nerve which is leaving the heart to run up the neck with the pneumogastric, entering the medulla by means of the superior laryngeal branch; for the *indirect* action of this nerve on the heart see p. 50. The depressor nerve is present as a distinct branch in the rabbit and cat, but in other animals it is mixed up with the vagus. Lastly, the cardiac branches contain fibres from the sympathetic which supply accelerator fibres to the heart (p. 49).

The pulmonary branches supply both sensory and motor branches to the trachea and motor fibres to the bronchi. Through these branches impressions are transmitted to the medulla by which the respiratory centre is regulated. Through other branches centripetal impulses are transmitted to the vaso-motor centre by which the general blood-pressure is regulated.

The thoracic œsophageal branches supply the œsophagus with motor power, so that division of the vagus causes food to accumulate in the lower part of the tube. The œsophageal nerves, after uniting in pairs in a peculiar manner, run along the œsophagus one superiorly the other inferiorly, and passing through the diaphragm they enter the abdominal cavity. The superior nerve supplies the left sac of the stomach and enters the solar plexus, from which it runs to the intestines and other organs (p. 206); the inferior nerve terminates in the walls of the stomach at its cardiac or right extremity.

Division of both vagi in the horse causes the breathing to become much deeper, more prolonged, and suffocation may result owing to loss of motor power in the larynx. Through the absence of sensation in the larynx, trachea, bronchi, and lungs, food is apt to find its way into the respiratory passages and produce pneumonia. The lungs likewise undergo congestion owing to the laboured and difficult respiration, and the parts become œdematous. In the horse the respirations have been known to fall to five per minute, but the heart beats rapidly owing to the unbalanced action of the sympathetic. Through paralysis of the œsophagus and stomach food collects in the latter, and may extend throughout the entire length of the œsophagus up the neck. Apparently engorgement of the stomach in the horse is not invariably produced as the result of dividing both vagi, for some observers have noted no difficulty in this respect. Experiments made by Colin show that division of the vagi paralyzes the stomach, so that poisons may remain there and cause the animal no inconvenience as they never pass into the intestine, and thus cannot become absorbed (see p. 176). This is a point of practical importance, and warns us how useless drugs administered by the mouth may be in some digestive troubles of the horse, especially those of the stomach.

Eleventh Pair, or Spinal Accessory, arise by two roots, one from low down the cervical portion of the cord, the other from the medulla. It is essentially a motor nerve, but through being intimately connected with the pneumogastric it also possesses sensory fibres. The use of this nerve is to supply motor power to the sterno-maxillaris, trapezius, and a portion of the levator humeri muscles: at its origin it supplies most of the motor fibres found in the vagus, and also furnishes the latter with its cardio-inhibitory fibres. The accessory is considered also to possess an influence over the larynx; division of it produces no difficulty in breathing, as in the case of the recurrent laryngeal, but it causes loss of voice due to paralysis of the motor fibres of the vagus.

Twelfth Pair, or Lingual.—The branches of this nerve supply the tongue with motor power, and fibres to the muscles which depress the larynx. Section of the nerve on both sides causes paralysis of the organ; dogs are unable to lap, and injure the protruding tongue with the teeth.

Medulla Oblongata or Bulb.

Situated at the top of the spinal cord, and forming the connection between it and the brain, is the medulla oblongata. It is composed of white and grey matter, but not arranged with the regularity found in the cord; the columns of the latter are continued into it, and give rise to certain columns in the bulb larger and more prominent than those of the cord. The inferior columns form the inferior pyramids of the bulb, the superior form the superior pyramids, and the lateral columns dividing into three parts help to form the restiform bodies.

As the main paths or highways in the cord are either going to or coming from the brain, it is interesting to study briefly their distribution in the bulb. Of all the paths known in the cord only three pass for certain through the bulb to higher centres in the brain, viz., the pyramidal tract the fibres of which are descending to the cord from their origin in the cells of the cerebral cortex, and the cerebellar tracts which pass upward through the medulla to reach the cerebellum.

The tracts passing through the bulb from the cerebrum decussate in the bulb, and in this way account for a right brain lesion producing a left body paralysis. All the other tracts in the cord terminate in groups of cells in the bulb, and act as carriers between it and the cord.

The grey matter of the cord does not maintain its characteristic appearance in the bulb, the inferior cornua disappear, while the superior cornua enlarge. Owing to the decussation of fibres in the inferior pyramid the grey and white matter get mingled up, and nuclei and masses of nerve cells are formed as the result; from these nuclei the cranial nerves arise. This arrangement leads to considerable complexity in the grey matter of the medulla, and a markedly intricate arrangement of the fibres of the white substance.

Centres in the Medulla.—The various centres found in the bulb are of such importance to life that an injury to this part generally means instantaneous death. The whole of the rest of the brain may gradually be removed without destroying life, but the medulla itself will not tolerate interference. The reflex and other centres are so numerous and widespread, that it is remarkable how the varied functions carried out by them can be performed within such a limited area. The centres localized in the bulb are those for mastication, swallowing, sucking, vomiting, respiration, phonation, coughing, the movements of the heart, bloodvessels, and iris, the secretion of saliva, the glycosuria centre, a centre for the sweat glands and a centre for shivering.

Though all these functions have been more or less clearly referred to the bulb, we must avoid falling into the error that a definite representation exists for each of them; and though the term centre is employed, it is more as a convenient mode of expression, than as absolutely establishing the fact that any particular group or groups of cells are responsible for one function more than another. Perhaps the only exception to this is the respiratory centre, which has been defined with a certain amount of exactitude.

The *mastication* and *swallowing centres* lie in the floor of the fourth ventricle; they have for their afferent nerves the inferior divison of the fifth, glosso-pharyngeal, and the superior laryngeal of the pneumogastric; whilst the motor branches are in the motor parts of the fifth for mastication, and in the fibres of the pharyngeal plexus of the vagus for swallowing. All the muscles of mastication, except the digastricus, receive motor nerves from the inferior maxillary division of the fifth pair. It would appear that the reflex act of swallowing is excited by the presence of food in the pharynx.

A *vomiting centre* exists in the bulb, which in the horse and ruminants is certainly most imperfectly developed. We have previously (p. 180) drawn attention to the fact that there is no drug which has the power of exciting vomiting in the horse; tartar emetic has not the slightest action, and the effect of apomorphia is only to produce the most alarming symptoms of cerebral excitement, but no attempt at vomiting. In the dog and pig the vomiting centre is well developed. The afferent nerves may be those of the pharynx, palate, and root of tongue, viz., the glosso-pharyngeal, or those from the mucous membrane of the stomach, for example, the vagus and sympathetic; the impression having been carried to the bulb the efferent nerves are the phrenics for the diaphragm, and vagus for the stomach and œsophagus. The vomiting centre may be directly stimulated by irritating the central end of the vagus.

Secretion of Saliva.—The centre for this lies in the floor of the fourth ventricle at the origin of the seventh and ninth pair of nerves. The afferent nerves are those of taste, viz., the gustatory branch of the fifth and glosso-pharyngeal, whilst the chorda tympani is not only afferent from the fore part of the tongue but is also the efferent nerve to the submaxillary, and the superficial petrosal that to the parotid gland. Other centres in the bulb are the cardio-inhibitory and respiratory centres.

For the *respiratory centre* see p. 108.

For the *cardio-accelerator* and *cardio-inhibitory centre* see pp. 48, 49.

For the *vaso-motor centre* see p. 75

For the *diabetic centre* see p. 230.

Functions of the Bulb.—The bulb apart from the brain cannot elaborate sensation or voluntary movement. It forms a pathway to the brain for the columns of the spinal cord, and is a conductor of centripetal and centrifugal impulses; it gives origin to all the cranial nerves but those of smell, sight, and the motor nerves of the eyeball; finally it is the supreme reflex centre for the nerves governing respiration, circulation, the action of the heart, and the digestive apparatus from the mouth to the intestine.

The **Pons Varolii** conducts centripetal and centrifugal impulses to and fro and up and down; it connects the cerebrum with the bulb and cerebellum, and several of the cranial nerves arise in connection with the grey matter of the various nuclei found in it. When stimulated, pain and muscular spasms are produced.

The **Thalami Optici** are connected with vision, but are mainly supposed to be the centres for tactile impressions which they transmit onwards to the cerebral cortex (Fig. 92, OT).

The **Corpora Striata** are interesting clinically on account of the comparative frequency with which they are diseased in the horse. They are considered to be the centres for co-ordination of motor impulses; when they are destroyed the animal has an irresistible tendency to move forwards. We have certainly seen this latter symptom shown in the horse in disease of the corpora striata, but it is far from invariable. It is remarkable how extensively the parts may be affected and pressed upon by tumours without symptoms being exhibited: the gradual progress of the pressure or destruction may account for this. The corpora striata are also considered to be concerned in heat production; there appears to be no doubt that experimental injury of these bodies produces a high temperature. Nothing is known of the mechanism, but it is supposed that impulses pass from the corpora striata to the muscles, the result being a great increase in the amount of heat produced. It is of interest to remember that the corpora striata, unlike the optic thalami, are shown by their developmental history to be really portions of the cortical grey matter.

Cerebellum.

In the cerebellum is found a collection of fibres and ganglion cells in communication with tracts from the spinal cord, bulb and cerebrum. It is the first piece of nervous tissue we have studied where the grey matter is externally placed and not internally as in the cord; the surface being folded and doubled in on itself to a considerable extent, thus forming convolutions.

The functions of the cerebellum are principally concerned in the co-ordination of movement, viz., harmony and rhythm in muscular actions; it is enabled to carry out this function through its connection with the superior columns of the cord, which keep the cerebellum informed of the position of the limbs. There can be no doubt that in co-ordinating muscular movement, the cerebellum is assisted both by the sense of sight, and by the nerves from the otolith organs and semicircular canals of the ear; an animal walks with uncertainty when the eyes are covered up, and disease of the internal ear is a well-known cause of vertigo in the human subject.

Injury of the cerebellum produces no sensory disturbance, but entails defects of movement. When sliced away in birds they lose the power of flying, walking, or preserving their equilibrium; there is no loss of consciousness or intelligence, but an inability to co-ordinate the skeletal muscles. Injury to one of the crura of the cerebellum produces 'forced movements' as they are termed. The animal rolls over and over around the long axis of the body, or else circus movements or somersaults are performed. In dogs superficial injury to one of the processes of the cerebellum causes only temporary disturbance, whilst deep injury or removal of a hemisphere causes rigidity of the legs and shaking of the head; more extensive injury is followed by disturbance of co-ordination. The entire cerebellum has been removed in the dog, the animal living for many months; in the first instance spasms of the muscles of the head, neck, and fore legs, and weakness of the hind legs were present; when the eyes were closed standing was impossible. These symptoms gradually gave way, and the animal was left with a deficiency of muscular tone, and a tremor in the muscles which increased on the performance of voluntary movement; it could swim but was muscularly weak, and eventually died from marasmus.

The cerebellum influences movement by re-inforcing the activity of the opposite hemisphere of the cerebrum (Luciani), especially of the 'motor area.' The movements produced by the opposite cerebral hemisphere become wanting in steadiness and power when half of the cerebellum has been removed, and the muscles innervated by that hemisphere are deficient in tone. No direct downward connection of the cerebellum with the cord is known to exist, though, as previously mentioned, the cord in an upward direction is connected with the cerebellum.

Mid Brain.

There is little of importance to the general student to be said about the physiology of the mid brain. The anterior corpora quadrigemina are concerned with the oldest primitive reflex centre, working from the optic nerve upon the eyeball muscles. The posterior corpora quadrigemina are important in the higher group of vertebrates, viz., birds and mammals which have a cochlea, that is, a 'hearing' ear besides an 'equilibrating' ear. The posterior quadrigeminal bodies receive fibres from the cochlea nerve, and have reflex centres connected with lower auditory functions.

For instance, a cat with the brain cut through just in front of the posterior bodies emits on stimulation of a hurtful kind to the skin a long angry vocalized note. But this ceases directly the section lies behind the posterior bodies. So also the 'chloroform cry' that animals and men give under chloroform goes on when the brain is cut in front of the posterior bodies, but not when the section is made behind them.

Cerebrum.

The cerebrum is composed of grey and white matter, the grey being externally placed and thrown into convolutions. These convolutions, though well marked in the lower animals, are by no means so numerous as in the man-like apes and man. The use of the convolutions is no doubt to increase the surface of the brain, and the deeper and more complex they are, the greater, as a rule, is the intelligence of the animal. In the horse the convolutions are comparatively very shallow.

Use of the Cerebrum.—In the grey matter of the cerebrum is located the seat of sensation, reasoning, and will. The white matter is simply the conducting paths along which the impulses are distributed.

It is quite possible for an animal to perform acts which look as if executed by intelligence, or to undertake movements which need precision, in spite of the fact that it is without a cerebrum. Some very curious observations have been made on the frog in which the cerebral hemispheres have been removed. If stimulated the frog springs, if thrown into the water it swims, if placed on its back it recovers its normal position, and if stroked it croaks. All these actions would indicate the presence of consciousness, but such is not so; the frog without its cerebral lobes will remain, unless stimulated, in one position until it dies, it appears to possess no power of spontaneous movement, or power of will. A remarkable experiment performed on a frog in this condition consists in placing it on a board which is gradually brought from the horizontal to the vertical position; during the movement the animal crawls up the inclined plane, and when the board is vertically placed it sits on the top perfectly balanced; as the board is lowered to the opposite side from which it was raised the creature descends. It is only during the time the board is being raised or lowered that the frog moves, but the movements are executed with precision. It is evident that these acts which strike one as being intelligent are really reflex, and are executed by the spinal cord, the animal being absolutely unconscious of what is going on, and it may be amongst even the higher animals that some acts regarded as volitional are in reality reflex.

Motor and Sensory Areas.—So far as we are aware no observations have been made on the motor and sensory areas of the cerebrum of Ungulata, but the dog has on this point been carefully examined.

The dog's brain is marked by two fissures known as the sulcus cruciatus (Fig. 98, S), and fossa Sylvii (Fig. 98, F). Between these fissures are arranged four primary convolutions I., II., III., and IV. (Figs. 98 and 99). In the anterior part of the fourth or superior convolution are found from before backwards—

(*a*) The motor areas for the muscles of the neck (Fig. 98—1). (*b*) The motor areas for the extensors and abductors of the fore-leg (Fig. 98—2). (*c*) The motor areas for the elevation of the shoulder and extension of fore-limb movements as in walking (Fig. 98—8). (*d*) The motor areas for the flexors and rotators of the fore-leg (Fig. 98—3). (*e*) The motor areas for the muscles of the hind-leg (Fig. 98—4). (*f*) The motor areas for the retraction and abduction of the fore-leg (Fig. 98—7). (*g*) The motor areas for the lateral switching movements of the tail (Fig. 98—6). Close to No. 2 area (Fig. 98) is one *d* (Fig. 99), stimulation of which causes the eye to turn to the opposite side, opens the eyelid and dilates the pupil. In the third convolution is situated an area 9, 9, 9 (Fig. 99), stimulation of which controls the movement of the orbicularis muscle, produces an upward movement of the eyeball,

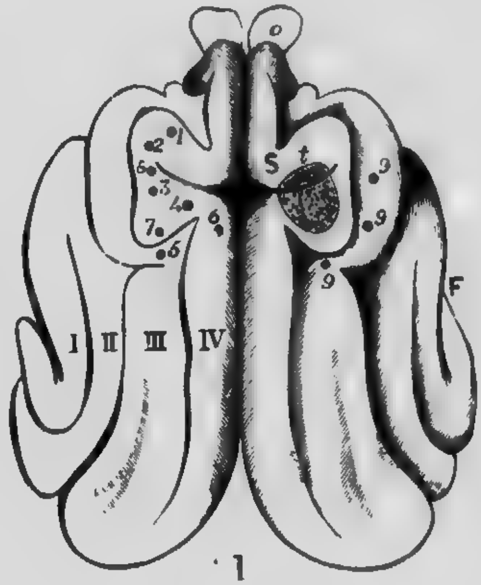

FIG. 98.

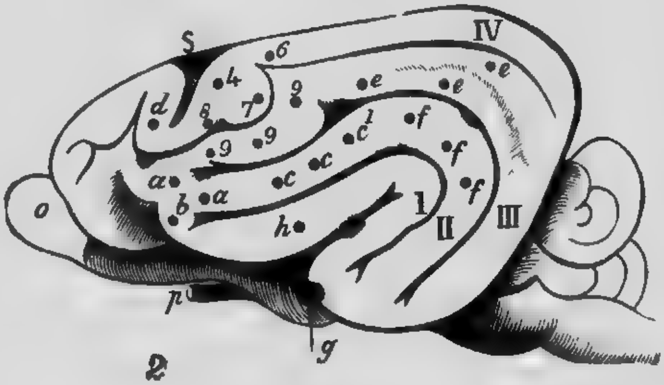

FIG. 99.

TO ILLUSTRATE THE MOTOR AREAS IN THE BRAIN OF THE DOG (LANDOIS AND STIRLING).

Fig. 98, cerebrum of the dog from above. Fig. 99, cerebrum from the side. I., II., III., IV., the four primary convolutions; S, sulcus cruciatus; F, sylvian fosse; *o*, olfactory lobe; *p*, optic nerve. The positions of the areas are described in the text.

and a narrowing of the pupil; behind this is *e*, *e*, *e*, an area which represents vision.

In the second convolution is an area *a a* (Fig. 99), which produces retraction and elevation of the angle of the mouth with partial opening of it. Behind this is *c c*, stimulation of which retracts the mouth owing to the action of the platysma; then an area c^1 which like 9 (Fig. 99) causes elevation of one angle of the mouth and of one half the face until the eye is partly closed. Behind this is *f f f*, which is the auditory centre.

In the first convolution is the oral centre (*b*, Fig. 99), stimulation of which opens the mouth, protrudes and retracts the tongue, while the dog not unfrequently howls.

All these centres have been indicated, but it is necessary to remember that though in area they may be as large as a pea, yet to an extent they overlap. The higher the animal is in the scale the greater the complexity observed in the areas, as for instance in the monkey, where the skilled movements of the hands and feet are largely represented in the cortex. The size of an area bears no relation to the size of the part supplied, but does bear a relation to the complexity of movement which the part is intended to produce. Thus the thumb area in the cortex of the monkey is relatively larger than the shoulder or hip area.

The effect of removing the motor areas differs according to the animal; in the monkey it results in permanent motor paralysis of hand or foot, but not of parts with less skilled movement, *e.g.*, shoulder or knee. In the dog paralysis is not necessarily produced, and it has been supposed that the basal ganglia are capable in this animal of taking on the duties of the cortex. The destruction which has been observed at times in the cortex of the horse is commonly unaccompanied by any symptoms until shortly before death.

Strong stimulation of the motor areas produces epilepsy. By observing the groups of muscles first affected and knowing the region of the cortex to which they are related, it is possible, certainly in man, to localize with considerable exactitude the seat of the trouble. Removal of the anterior or frontal convolutions in the dog leads to unilateral motor and sensory paralysis, from which the animal recovers with the exception that there is loss of muscular sense. If the operation be performed on both sides there is an exaggeration of the symptoms, and the animal becomes vicious. Removal of the posterior or occipital lobes leads to blindness, no loss of motion or of muscular sense, and the dog remains obedient but sluggish. Removal of a large mass of cerebral cortex causes the animal to become intensely stupid, it walks slowly, the head hangs down, sensibility is diminished; the dog sees but cannot comprehend, it howls from hunger and eats until its stomach is full, it exhibits no sexual excitement, and becomes, in fact, an eating, complex, reflex machine.

Colin draws attention to the difficulty in producing paralysis experimentally in the horse from lesions of the hemispheres. Neither the artificial production of a clot in the falciform sinus, nor the introduction of pieces of lead the size of a pea into the convolutions, gave rise to hemiplegia. This quite bears out what we know to be a clinical fact, that it is possible for horses to have in their lateral ventricles tumours the size of an egg without producing any disturbance. We have seen such cases, the tumours being of variable size, and the clinical history has never given more than a few days' illness, though the growths must have been forming for a considerable period.

The **Circulation in the Brain** is peculiar; the veins or so-called sinuses are enclosed in very rigid membranous walls formed by the dura mater; the blood is driven through these not only by the force from behind, but by the aspiratory effect produced by inspiration (see also p. 82).

Coverings of the Brain.—The dura mater is a dense fibrous membrane, which acts the part of a protective covering for the brain; between it and the arachnoid a lymphatic space known as the subdural exists. The arachnoid contains but few vessels and no nerves, and covers the extremely vascular pia mater; between these is formed the subarachnoid space, which contains the subarachnoid or cerebral fluid.

Cerebral Fluid.—The subarachnoid space communicates with the ventricles of the brain, the lymph in it is also shown to be in communication with the perivascular spaces of the cerebral vessels and the lymphatic spaces in the perineural covering of nerves. Through the fourth ventricle it communicates with the central canal of the spinal cord, and there is also a connection between the cerebral spaces and those formed on the exterior of the cord. The subdural and to an extent the subarachnoid fluid communicates with the sinuses of the dura mater. The cerebral fluid is secreted by the pia mater and choroid plexus. The use of this cerebral fluid, which normally in horses amounts to 80 or 90 grains, is to equalize the pressure on the brain, afford protection to the latter, and through the manner in which the organ is suspended inside the skull by the dura mater, to save it from jar and concussion; both cerebrum and cerebellum half float on water-cushions. Withdrawal of the cerebral fluid leads to convulsions, and an increase in the amount may cause coma owing to the pressure it exercises.

Movements of the Brain.—When the brain is exposed it rises and falls during each respiration, rising with expiration and falling during inspiration; the cause of this is the respiratory rise and fall of blood pressure. Alterations in the volume of the brain have been observed; the brain expands under a rise in pressure of the systemic arteries, such as is produced by stimulating the central end of the sciatic. Ether and particularly strychnin causes a considerable expansion; chloral hydrate and especially chloroform cause a marked contraction. No vaso-motor fibres have been discovered acting in the brain.

The Sympathetic System.

An extensive system of nerves exists in the body, the function of which is mainly to supply the bloodvessels, viscera and glands. At one time, owing to its peculiar distribution, the sympathetic system was regarded as distinct from the cerebro-spinal; this is now known to be incorrect; the two are intimately connected.

The sympathetic is composed of nerves and ganglia; the nerve fibres are remarkable for their fineness and are both medullated and non-medullated; the ganglia consist of multipolar cells and nerve fibres. The numerous processes belonging to the cells serve to increase the number of tracts along which impulses travel, so that these are able to pass out in several directions. There is no evidence that these ganglia can originate impulses, but they serve to transmit nerve impulses. Until lately there was nothing to show that they were capable of performing a reflex act, but this would now appear to be possible, although in a peculiarly simplified way.

Medullated nerves by passing through a sympathetic ganglion lose their medulla, and Langley has shown that nearly all the nerve fibres entering a ganglion terminate in the nerve cells of that ganglion, though some pass through without communicating with the cells. Nicotin applied to a ganglion paralyzes the cells but not the nerve fibres. By this method of inquiry, which is due to Langley, it is possible to demonstrate what nerve fibres do and what do not end in the various sympathetic ganglia. The number of fibres in a nerve is increased by passing through a ganglion, and further, the ganglion exercises a nutritive effect over such of the nerve fibres as are branches from the cells of the ganglion.

Gaskell has shown that the extensive sympathetic system is capable of classification into three groups: (1) *Vertebral ganglia*, which run on either side of the vertebral column practically throughout its length. Below and in connection with these are the large nervous plexuses and ganglia of the chest and abdomen, such as the cardiac, solar, and mesenteric plexuses. These are known as (2) the *Collateral ganglia*; from these are given off fibres which terminate in the tissues supplied by them, and are known as (3) *Terminal ganglia*. On reference to Fig. 85, p. 394, this distribution is shown in a diagrammatic form, Σ being the vertebral, δ the collateral, and δ′ the terminal ganglia.

It is through the vertebral ganglia that the sympathetic is mainly brought into connection with the cerebro-spinal system. White medullated nerve fibres run out from the spinal cord, especially in the dorsal and lumbar regions, to join the ganglia on the vertebral chain; this branch is known as the *white ramus communicans* (V, Fig. 85). After passing through the vertebral ganglia it loses its medulla, and a branch, the *grey ramus communicans* (rv, Fig. 85), leaves the ganglion, returns to the spinal cord, and again issues from it in a manner previously described (p. 77), to supply the bloodvessels of the spinal cord, and those of the fore and hind limbs with constrictor influence. Those fibres of the white ramus which do not return pass through the vertebral ganglia, become non-medullated, and join the collateral ganglia. White rami are found running out from the spinal cord of the dog from the second dorsal to the second lumbar nerve; in front and behind these points there are no white but only grey rami. In the cervical region, though there is no white ramus yet fibres run out from the cord by means of the spinal accessory nerve, a division of which enters the vagus and supplies the heart with inhibitory nerves (Fig. 15, p. 46); from the second and third dorsal nerves white fibres are given off which pass through vertebral sympathetic ganglia, and finally reach the heart, exercising an augmentor effort (Fig. 15). In the cervical sympathetic fibres are found supplying constrictor influence to the bloodvessels of the head and neck, dilator fibres for the iris, fibres causing the eyelids to open, the eyeball to come forward, and the third eyelid to be retracted in the cat, dog and rabbit; besides these there are sweat fibres for the head and neck, secretory fibres for the salivary glands, and for the glands in the muzzle of the ox. In both the ox and dog trophic fibres are found supplying the muzzle, and in the horse there are fibres for the sebaceous glands of the skin of the ear.

Arloing has shown that in both the ox and dog division of the cervical sympathetic has been followed by a dry, papillated, and hypertrophied condition of the skin of the nose and muzzle, due to damage to the trophic fibres.

From the spinal cord between the sixth and thirteenth dorsal and the first and second lumbar nerves in the dog, the greater and lesser splanchnic nerves are given off, which run to collateral ganglia, the solar plexus; from the first to the third lumbar nerves in the dog fibres are also given off which form the inferior mesenteric ganglion (see Fig. 55, p. 206). From these plexuses fibres are given off supplying the muscles of the stomach and intestines with inhibitory power, so that stimulation of the splanchnics causes the viscera to cease moving (see p. 205). The splanchnics are also the chief vaso-motor nerves to the vessels of the abdomen; section of them gives rise to great dilatation of the vessels of the intestines, liver, kidneys, etc., due to vaso-motor paralysis, and so causes a great fall in blood pressure; stimulation of the peripheral end of the divided nerve causes the vessels to contract and raises the general blood pressure. The splanchnics contain sensory fibres; it is through these that abdominal pain is felt. For further remarks regarding the nerve supply of the viscera, see p. 205. The sympathetic system also furnishes the pilo-motor fibres in the cat and dog (see p. 276).

The functions of the sympathetic may thus be summarized: This nervous system supplies the bloodvessels with constrictor and dilator fibres, the viscera with motor and inhibitory fibres, accelerator fibres to the heart, dilator fibres for the pupil, secretory fibres for sweat, salivary, and sebaceous glands, motor fibres to the muscles of the hair, and fibres which exercise an effect on the nutrition of a part.

Psychical Powers.—In attempting to define to what extent the faculty of reasoning exists in animals, we are treading on distinctly controversial ground. Probably this question can only be positively answered in the affirmative for two animals, viz., the elephant and the dog. With the horse the moral sense is very small; we do not think he knows he is doing anything wrong when he kicks his stable down once or twice a week, or when he 'runs away,' but he does understand that he should not refuse a jump, and a horse careless in his walk or trot knows exactly what every stumble will be followed by, and anticipates matters accordingly.

Strength of will most animals lose as the result of domestication. They become mere reflex machines or automata, but there are notable exceptions, for instance the ass, mule, and occasionally the horse. The so-called stupidity of the ass and provoking obstinacy of the mule are not indications of want of intelligence, on the other hand they show a determination of purpose and strength of will, which if these animals understood how to combine against man, would obtain for them their complete freedom from civilization.

The majority of horses on the other hand have no great strength of will; they can be rendered docile and tractable, they will gallop until they drop, work at high pressure when low would suffice, can never apparently learn the obvious lesson that it is the 'willing horse' which suffers, and that the harder they work the more they get to do. All this is due to defective intelligence and a want of the higher faculties; they cannot reason like the dog or elephant, and are more flexible than the ass or mule.*

Some horses do show signs of reasoning and are capable of grasping a position. A load so heavy as to be beyond the limit of his power, or from some other cause, has taught him to refuse to work; to use the familiar expression, he

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* We are aware that the majority of people will not agree with these views of the defective intelligence of the horse, but we are not alone in our judgment; see 'The Points of the Horse,' by Captain Hayes, whose experience amongst horses in all parts of the world was very considerable.

MICROCOPY RESOLUTION TEST CHART

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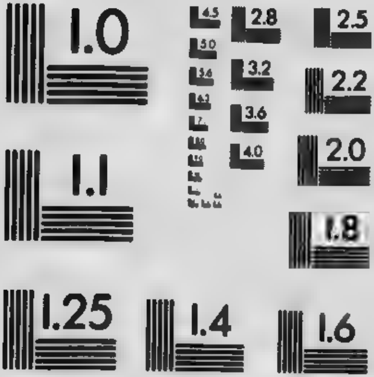

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'jibs,' he has learned to disobey, he has learned his own strength, and the comparative powerlessness of his master, and this through an exercise of reason. In other words, the horse which refuses to wear himself out in the service of man is one possessing too much intelligence and strength of will for a slave; a 'jibber' is an intelligent and not a stupid horse.

As a rule the intelligence and affection of the horse only exist in books and the imagination of those who have the least to do with him; whatever region of the brain affection is located in, it does not occupy much space in the equine. Taking the dog as the standard to judge by, it may be said with the greatest truth that the large majority of horses have no affection whatever, either for their own kind (excluding maternal affection) or for human beings. Two strange horses cannot as a rule be put together without disagreeing, and no one ever heard of a horse pining away through the prolonged absence of his master! The often quoted example of a horse jumping over a man on the ground rather than treading on him is an act misunderstood; it is true the horse jumps over the man, but he does so because he is taught to jump over every obstacle, and the man on the ground might for all he knows be a bush. In other words it becomes largely a reflex action, and only to a very limited extent a volitional act.

If the horse possesses but little affection it is compensated for by cherishing no resentment; he will kick his friend as readily as a foe, or in many cases his groom with as much cheerfulness as a perfect stranger; to all his hard life and the abominable cruelties of domestication he shows no sign of resentment; water and feed him, and give him a place to lie in, and he forgets the past in his anxiety for the present. He is a peculiar mixture of courage and cowardice; physical suffering he can endure, no animal bears pain better; when his blood is up nothing is too big or too wide for him in the hunting field, and he has a keen enjoyment for both chase and race in spite of the punishment they may entail. But the same horse is frightened out of his life by a piece of paper blowing across the road, or at his own shadow, and an unusual sight or a heap of stones on the side of the road has cost many a man his life. No animal is more readily seized with panic, and this spreads amongst a body of horse like an electric shock.

The horse has an excellent memory for locality, probably nearly equal to that of the dog or cat; he never forgets a road, and automaton-like, if he has once stopped at any place on it, he wants to stop at the same place next time no matter how long the interval may be between the visits.

Reasoning power in the majority of horses is small; an animal runs away because he is seized with panic, or his spirits are bubbling over, but with few exceptions distinct acts of reasoning are rare. Of this we daily see examples in our infirmaries; horses injured in the most severe manner through their own struggles when placed in a little difficulty, such as a head rope around the leg, or an inability to rise when down owing to being too close to the wall, or some trifling circumstance of this kind, where if he employed any reasoning powers he would remain quiet until released, instead of which he behaves like a lunatic, inflicting in a short time injuries which may lay him up for months. Or take the case of a horse which gets his tail over the reins when being driven; instead of lifting the tail in response to the exertions of the driver he draws it closer down to his quarters, gripping the reins as in a vice, and is so astonished and frightened at the new state of things that he becomes uncontrollable. We can hardly point to a single act in the horse in which the powers of reasoning are clearly brought into play, unless it be that he knows punishment follows refusal to obey, and often learns to 'jib.'

The horse is very conservative, he likes nothing new nor any departure from his ordinary mode of life; he will starve himself for days rather than take a new feeding grain, and he dislikes a change of stable or a new place. His gregarious instincts are proverbial; he frets at the absence of his companions, and if used to work amongst a body of horses, as in cavalry, he will take any degree of punishment rather than leave them for five minutes. During the absence of his companions he neighs, sweats, paws with the fore legs, and almost screams with delight on rejoining them, not because he loves them, but because he dislikes being alone.

Finally, his predominant feature, and the feature of all animals below adult man, is the childishness present throughout life; probably the absence of care, worry and anxiety may account for this. The horse will play all day with a piece of rope, or nibble his neighbour persistently; even the oldest horses when 'fresh' will perform the antics of a foal, and imitation amongst them is so great that if one of a string of horses being led along happens to kick out, this repeats itself all along the line as if by preconceived arrangement.

Sydney Smith defined the difference between reason and instinct as follows: 'If in order to do a certain thing certain means are adopted to effect it, with a clear and precise notion that these means are subservient to that end, the act is one of reason; if, on the other hand, means are adopted subservient to an end, without there being the least degree of consciousness that these means are subservient to the end, then the act is one of instinct.' Morgan* believes that between instinct on the one hand, and reason on the other, we may insert as a middle term 'intelligence,' while Romanes and others use the word 'intelligence' as synonymous with 'reason.' Morgan defines instinct as a motor response to a certain stimulus, *i.e.*, a reflex act, but one accompanied by consciousness. Animals come into the world endowed with this innate capacity for motor response; but these instincts are not quite perfect, they need training and experience, and their instructor is 'intelligence.' Intelligence, according to this observer, does not imply a conscious knowledge of the relation between the means employed and the end attained; such a conscious knowledge would be reason.

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* *Fortnightly Review*, August, 1898. It is from Professor Morgan's paper that we have obtained the views of Sydney Smith and Romanes.

We are asked, in other words, to regard animals as simply reflex machines, their brain being very little higher in the scale than their spinal cord, and for some animals such a position probably meets their case, but certainly not for all. If we accept Morgan's definition of instinct and intelligence, it offers no reasonable explanation why dogs fight, and why they worry cats; why a horse so inclined will turn his quarters towards another as he passes and rapidly let both hind legs fly in the direction of his objective; nor will it explain why a horse will use his fore legs to strike when he knows his hind legs cannot reach the object of his irritation. It is absolutely impossible to believe that such acts imply no conscious knowledge of the relation between the means employed and the end attained.

The higher animals are capable of a limited amount of reasoning; with some it is even well developed, with others it is extremely imperfect. The elephant and dog occupy the top of the scale, the ox and sheep the bottom, the horse comes midway. We do not see how to separate reason from intelligence, but there is no difficulty in separating them from instinct.

Animals are born with such complicated reflex acts as walking, galloping, jumping, etc., so highly developed that they are employed at once. No member of the human family has been seen to walk and run about a few hours after leaving the womb, for both brain and spinal cord are incompletely developed, and the acts have to be learned. This is not so with animals (excepting the dog and cat): foals, calves, lambs, goats, etc., are born prepared to feel their feet at once, they require no teaching and no imitation, their senses are perfect, they can recognize their mother or a stranger, can see, smell, hear; in fact they have nothing to learn, for they are born with as much intelligence as their parents, and only differ from them in one respect, and that is they are born wild, and so have to learn confidence. Domestication and obedience are not properties transmitted from parent to offspring.

CHAPTER XV

THE SENSES

SECTION I.

Sight.

THE delicate structures composing the eye receive a very thorough protection by the anatomical arrangement of the parts. The orbital cavity, for example, is nearly surrounded by incomplete bony walls, and the layers of fat within it assist the muscles in protecting the globe and the optic nerve. The eyelids sweep the cornea and protect the part from dust and exposure, the tears keep the face of the cornea brilliant; the *membrana nictitans* moves particles of solid matter which would otherwise produce irritation, and the eyeball can be retracted to a considerable extent to assist it in withdrawing from injury. The size of the orbit is such that ordinary blows inflicted upon the eye are expended on the margin of the orbital cavity, and not on the eyeball itself, so that the risk of serious injury is far less from large than from small bodies. The shape of the eyeball is not (in the horse) quite spherical, the vertical axis is greater than the horizontal, and the posterior face of the eyeball is distinctly flatter than the anterior.

Structure of the Eye.—Issuing from the back of the eyeball, very low down and inclined to the temporal side of the globe, is the *optic nerve,* which after describing a peculiar curve upwards, runs in the substance of the retractor muscle to enter the cranium through the optic foramen. This curve in the optic nerve (Fig. 100) is necessitated by the horizontal movements of the eyeball; if the eye looks backwards the curve is increased, whereas if it looks forwards the 'slack' is taken out of the nerve and the curve entirely disappears. The optic or second cranial nerve has a deep-seated origin in the corpora quadrigemina, and a representation in the occipital region of the cerebral hemispheres (see Fig. 99). The fibres forming the optic nerve decussate, those from the left brain passing to the right eye and vice versâ. In some animals this decussation is complete, such as the horse, sheep, and pig; but in others a certain number of fibres decussate, whilst some enter the nerve on the same side of the brain as that on which they originate; this is the arrangement in the dog, cat, rabbit, monkey, and man. This partial decussation is considered in man to play an important part in the production of sympathetic ophthalmia, the inflammatory trouble running along the optic nerve to the commissure, and so finding its way to the other eye. It is quite certain that in the horse, where the decussation is complete, sympathetic ophthalmia from an injury is unknown. Division of the optic nerve causes no pain but only the sensation of light; stimulation of the nerve causes flashes of light to be perceived by the brain—in fact the optic nerve conveys nothing but impulses which, when they reach the brain, give rise to that altered state of consciousness known as vision. Moreover, as we shall presently point out, the place where the optic nerve enters the eye is blind.

The globe of the eye is anteriorly made up of a transparent convex surface known as the *cornea*, whilst the remainder of its walls are opaque and formed by the *sclerotic*, *choroid*, and *retina*. The sclerotic is the tunic on which the strength of the eyeball depends, the choroid may be regarded as that which principally attends to the vascular supply, while the retina is the sensitive expansion of the optic nerve on which the picture is imprinted, and thus gives rise to sensory impressions.

The shape and tension of the eyeball is maintained by means of its humours, which are known as the aqueous and vitreous. The *aqueous humour* occupies the space between the cornea and the lens. It is a watery fluid, poor in solids, and is in reality lymph. It is constantly being secreted, probably by the ciliary processes, and as constantly carried away by the lymphatic channels with which it communicates through the spongy *ligamentum pectinatum;* these channels empty themselves into the anterior system of veins. If the anterior chamber be experimentally evacuated it is refilled in about twenty-four hours. The use of the fluid it contains is to maintain the convexity of the cornea; after death the process of drainage still appears to occur, though, of course, there is no reproduction, the result being that in a day or two the cornea flattens through loss of the aqueous humour.

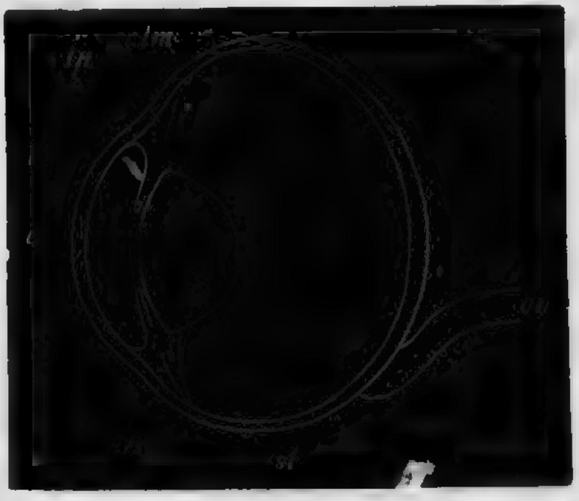

FIG. 100.—VERTICAL SECTION OF THE EYE OF THE HORSE, NATURAL SIZE.

c, Cornea; *l*, lens; *i*, iris; *cp*, ciliary process; *lp*, ligamentum pectinatum; *cl m*, position of ciliary muscle; *sl*, suspensory ligament of lens; *on*, optic nerve showing its curve.

The *vitreous humour* is a viscid, tenacious material, contained within the hyaloid membrane, which permeates its substance. The vitreous contains mucin and a very small percentage of solids. The use of this fluid is to maintain the intra-ocular pressure, by which the proper tension of the globe is brought about. The whole of the vitreous chamber is rendered dark by the liberal application of pigment, with the exception of a surface above the optic nerve which is brilliant and iridescent in appearance, and is known as the *tapetum lucidum*.

Between the two humours a diaphragm is situated known as the *iris*, which regulates the amount of light passing into the eye, and behind this is a focussing arrangement or *lens*. The cornea, lens, and humours constitute the refracting apparatus of the eye.

By means of the muscles of the eye the globe is given a considerable range of movement, and in addition it can be retracted within the orbital cavity; further, these muscles afford some protection to the optic nerve.

The similarity in construction between the eye and the apparatus known as a camera is very marked; both have a refracting surface anteriorly placed, a diaphragm to cut off superfluous rays of light, an arrangement for focussing, a dark chamber in which is placed a sensitized surface, and on which a reduced and inverted image of the picture is impressed.

Though we have thus briefly run over the leading features of the eye, yet there are certain of these structures which need some detailed description if we are to understand clearly the phenomena attending perfect vision.

The *Cornea* in most animals is circular in outline, in the horse it is somewhat oval; when viewed from the front and divided into two halves by a vertical line, it is distinctly larger on its nasal than on its temporal side. It is a very tough, non-vascular membrane, richly supplied with nerves, and nourished by the lymph which freely circulates in it. It may be regarded as the chief refractive apparatus of the eye. When viewed from the side the cornea is seen to be convex; measurement shows that in the majority of horses the curvature of the cornea taken in its horizontal and vertical meridians is not exactly the same as it would be supposing its surfaces were accurately spherical. The excess of curvature of one meridian of the cornea over that of the surface at right angles to it produces a defect in vision which is known as *astigmatism;*

the meridian in the horse which is nearly always the flattest is the horizontal.

The *Lens* is composed of various onion-like layers of different refractive powers. In shape it is bi-convex, the convexity of its posterior face being greater than that of the anterior. It is held in its place by a capsule which really suspends the lens in the eye, the capsule receiving attachment to some long processes behind the iris known as the *ciliary processes.* In the horse the lens is in contact with the ciliary processes, in most other animals there is a small space between the two. The lens possesses inherent elasticity, which admits of its surface undergoing an alteration in shape, so as to be flatter at one time, more convex at another. This alteration in shape occurs through the ready manner in which the lens by its elasticity yields to the pressure exercised on it through its capsule, so that if the tension of the capsule be relaxed the lens bulges, or if the tension be increased it flattens. In this way the eye is focussed or accommodated to various distances, a subject which will be dealt with presently.

The *Iris* is a curtain with a hole in the centre called the pupil. The shape of the pupil varies in different animals; in the dog it is circular, in the horse, sheep, ox and cat elliptical; in the latter animal the elliptical slit is placed vertically, in the others horizontally. The iris is mainly a collection of bloodvessels and muscular fibres, the whole being heavily coated with a brown pigment in the horse, though occasionally this is wanting, giving it a bluish-white streaky appearance, as in the so-called 'wall-eyed' horse. In the ox and dog the iris is a brighter brown than in the horse, while in the sheep it is brownish-yellow. The muscular fibres of the iris are commonly described as circular and radiating; a contraction of the circular muscle contracts the pupillary opening, a contraction of the radiating fibres dilates it. Langley and Anderson from their observations on the cat, dog, and rabbit, have proved that a dilator muscle to the iris exists; this question was for a long time in dispute. It is now accepted that dilatation of the pupil is due to the influence of a dilator muscle and inhibition of the circular muscle.

The nerve supply to these circular and radiating fibres is not the same; the circular fibres are supplied with motor power through the third cranial nerve, whilst the dilator muscle is supplied by the sympathetic. The latter fibres emerge from the spinal cord at the first three thoracic spinal nerves, from a part known as the cilio-spinal centre; from here they travel up the neck in the cervical sympathetic, and reach the iris through the ciliary ganglion. If the third nerve be divided the radiating muscular fibres of the iris contract under the unbalanced action of the sympathetic, and thus dilate the pupil; if the sympathetic be divided the pupil contracts under the unbalanced action of the sphincter fibres.

Stimulation of the retina by light is the natural method by which alterations in the size of the pupil are brought about, the act being reflex; in a brilliant light the pupil contracts, in a low light it dilates. In the horse this is not strictly true; in direct sunlight the pupil of this animal is a mere narrow chink, but in ordinary daylight it barely responds, or if it does contract it is so little as not to materially reduce the size of the pupil. Even when the light is concentrated on the eye, either by means of a mirror or a lens, the iris practically remains unchanged. Owing to this fact the eye of the horse can be examined by the ophthalmoscope without the use of atropin, or even without artificial light, in fact, under artificial light the pupil dilates. There are certain drugs which dilate the pupil such as atropin and cocain, and others which contract it, for example, morphia and eserin. It is curious to observe in the horse that although the pupil, when normally contracted, is elliptical, yet when it is dilated by atropin it becomes circular; the chief radiating fibres would therefore appear to be above and below and but very few on the sides. Eversbusch* has studied the structure of the iris of the horse, and states that the elongated form of the pupil is due to the presence of an accessory apparatus on the posterior surface of the iris, which he calls the *ligamentum inhibitorium;* through this ligament the sides of the iris are not pulled in by the contraction of the sphincter muscle. The long axis of the pupil in the horse is always horizontal, or practically so, no matter what the position of the head may be; this is a point which will be touched on again in dealing with the muscles of the eyeball. The pupil of the horse dilates moderately after the animal has been galloped; *immediately* after a violent death it dilates widely, but in the course of twenty-four hours or so, it gradually contracts until the pupil becomes a mere slit.

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* *Zeitschrift für Vergleichende Augenheilkunde*, Heft 1, 1882.

In the horse there exists on the edge of the iris, at the centre and upper part of the pupil, one or more large soot-like bodies known as *corpora nigra;* a small one may be found on the lower margin of the iris, but the upper ones are the most prominent. When the pupil is strongly contracted in direct sunlight, the centre of it is entirely blocked out by these pigmentary masses, and divided into an inner and outer portion. It would appear as if this caused an imperfect image to be imprinted on the retina, and this view we at one time held, but on subjecting the question to actual experiment no broken image was found to result from the use of a diaphragm the centre of which was blocked out. The use of these bodies is doubtless to assist in absorbing rays of light, but their position in the centre of the pupil would not appear theoretically to be the most suitable position, and they must have some other function. The horse, as far as we know, is the only animal possessing them.

Ligamentum Pectinatum.—Around the attached margin of the iris, viz., at the corneo-scleral border, a peculiar spongy tissue exists which gives the iris at this part a distinctly elevated rim; this is known as the ligamentum pectinatum. Roughly speaking it is a rim of spongy iris traversed by canals, crevices, and spaces, which lead into the lymphatic system of the eye; the function of this tissue is to carry off the aqueous humour as rapidly as it is worn out and replaced, by which means the normal tension of the anterior chamber is maintained.

The *Choroid* coat contains the vessels which nourish the retina; it possesses innumerable nerves, numerous lymphatics, and further it is an elastic coat. Anteriorly behind the iris it forms the peculiar folded structure known as the ciliary processes, and in front of this it furnishes the tissue which is called the iris; the iris and ciliary processes are therefore part of the choroid coat. With the exception of one area the whole of the interior of the choroid is covered with pigment, and the same extends on to the processes and iris. The area which is an exception lies on the posterior wall of the eyeball above the optic nerve; it is of a brilliant colour, being a mixture of green, yellow, and blue, and is known as the *tapetum lucidum.* This is found in both herbivora and carnivora; in the former it is due to the interference of light causing iridescence, produced by the arrangement of the connective tissue fibres of the choroid, and not to the presence of any pigment; in carnivora it is due to minute crystals in the cells of the part, the crystals causing the interference. The use of the tapetum is generally supposed to be to enable animals to see in the dark; this of course is impossible, but it is probable that the presence of a tapetum may enable an animal to see better in a dim light.

The *Ciliary Zone* is a peculiar and important part of the eye, formed on the one hand by the junction of the cornea and sclerotic, and on the other by the iris and ciliary processes. Between these lies a muscle known as the ciliary, which is firmly attached to the corneo-scleral margin, and runs backwards into the choroid, where it is attached. In man the *ciliary muscle* consists of both circular and longitudinal (or meridional) fibres; in the horse, and probably all the lower animals, only meridional fibres exist. The muscle is composed of unstriped fibres, and its use is to pull the choroid forward; the object of this will be apparent when we discuss the question of accommodation.

The *Vitreous* humour is enclosed in the hyaloid membrane: anteriorly this membrane, here known as the *Zonule of Zinn*, becomes dovetailed into the ridges formed by the ciliary processes, and enveloping the lens forms its suspensory ligament. If the amount of vitreous humour present is sufficient in quantity, this ligament of the lens must always be tense, and as it is very inelastic it tends to keep the lens flattened; we shall refer to this again in speaking of accommodation.

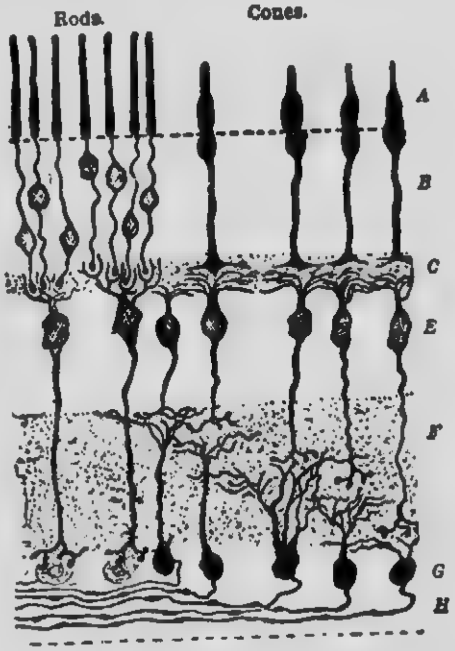

FIG. 101.—DIAGRAM OF STRUCTURE OF RETINA (BOWDITCH, AFTER CAJAL).

A, Layer of rods and cones; *B*, external nuclear layer; *C*, external molecular layer; *E*, internal nuclear layer; *F*, internal molecular layer; *G*, layer of ganglion cells; *H*, layer of nerve fibres.

The *Retina* lies within the choroid and outside the vitreous humour; it spreads out from the entrance of the optic nerve of which it is the expansion. Microscopic examination shows this membrane to be composed of seven layers (Fig. 101), of which the most important is one termed from its appearance the layer of rods and cones. It has been shown conclusively that these rods and cones are the essential elements of the retina, and that wherever they are absent the part is insensitive to light, as, for example, at the entrance of the optic nerve which forms the *blind spot.* Though the layer of rods and cones is the most important it is not placed as one would suppose, next the vitreous humour, but next to the choroid, whilst the layer next to the vitreous humour is composed of nerve fibres and ganglion cells. Rays of light have, therefore, in the first place to pierce the entire thickness of the retina to arrive at the rods and cones; here they give rise to a nervous impulse which retraces its steps in the retina, until it arrives at the layers next the vitreous humour, from which it is carried off by the optic nerve to the brain. In one sense the most important layer of the retina is the one composed of the rods and cones, since it effects the primary conversion of light-vibrations into visual impulses. Each cone is connected with a single nerve cell, but there may be several rods to one nerve cell; the cone is, therefore, considered to offer a more direct conducting path than the rods.

Visual purple or *Rhodopsin* is a curious red pigment existing in the eye; it is found in the rods but not the cones of the retina. This colouring matter is readily decomposed by light, and is consequently always being produced. It is possible by keeping an animal in the dark in order to increase the visual purple, to procure then a picture on the retina through its decomposition on exposure to light. It is believed that the vision of night-seeing animals is mainly brought about by the rods in virtue of their visual purple, while the cones are adapted for daylight. Visual purple on the rods increases their irritability in dim lights. At the same time it is quite certain that visual purple is not essential to vision, for there is none in the fovea of the human eye, the area of the most acute vision, and none in certain birds, reptiles, and bats. In people totally colour-blind vision must be carried on by the rods, as it is supposed that the cones are the seat of colour perception.

The entrance of the optic nerve within the eyeball is spoken of as the *optic disc* or *papilla*; it is a concave oval surface surrounded by a white ring formed of sclerotic. lies, in the horse, towards the bottom of the eyeball and inclined to the temporal side. This region is blind owing to the absence of rods and cones.

There is no *yellow spot* in animals; in man this exists, and the area which it encloses, the fovea, is that of the most acute vision. In the fovea all the other retinal layers but that of the cones have disappeared; there are no rods in the yellow spot or fovea of man. Reptiles possess only cones in their retina, and both birds and fishes have more cones than rods. A line drawn through the centre of the cornea to the yellow spot is called the visual axis of the eye. The visual axis in man does not quite agree with the optic axis, viz., a line drawn exactly through the centre of curvature of each refractive medium. In the lower animals we have no means of knowing whether the optic axis is also the visual axis, but from the absence of the yellow spot it is assumed to be.

There is, however, an area of acute vision in the horse, and the animal brings it into play by raising the head very high, and protruding the muzzle so as to render the face horizontal.

The Ophthalmoscope.—We may here describe in outline the theory of this instrument, and the appearance of the picture presented by it. To examine the eye, a mirror with a hole in the centre is applied to the eye of the observer so that he can see through the hole into the observed eye; from a suitable source of light, rays are reflected by the mirror through the pupil on to the retina to be examined. When light is thrown into the eye, the rays are reflected back through the pupil in the direction in which they entered, and pass through the hole in the mirror into the eye of the observer. On looking at the retina of the horse, a brilliantly coloured surface is seat of

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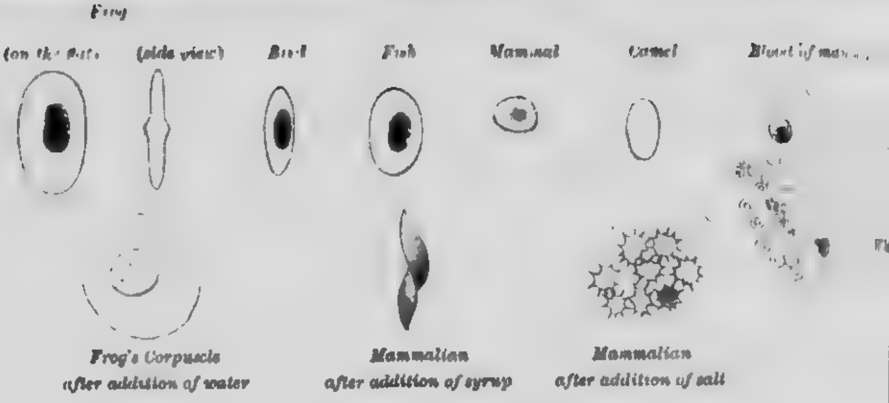
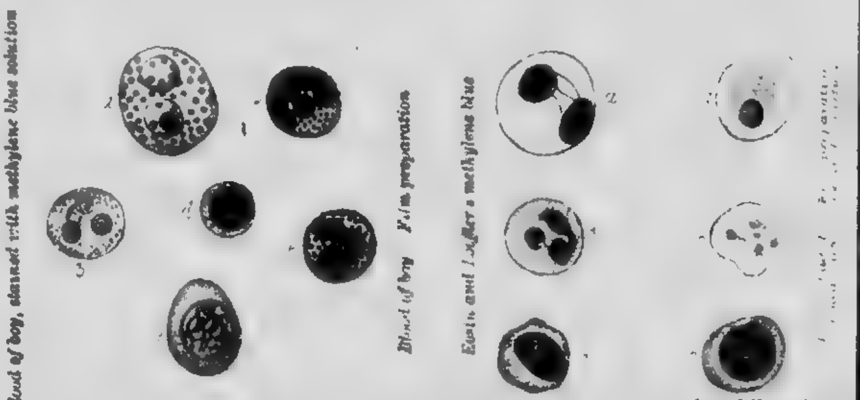
PLATE I.

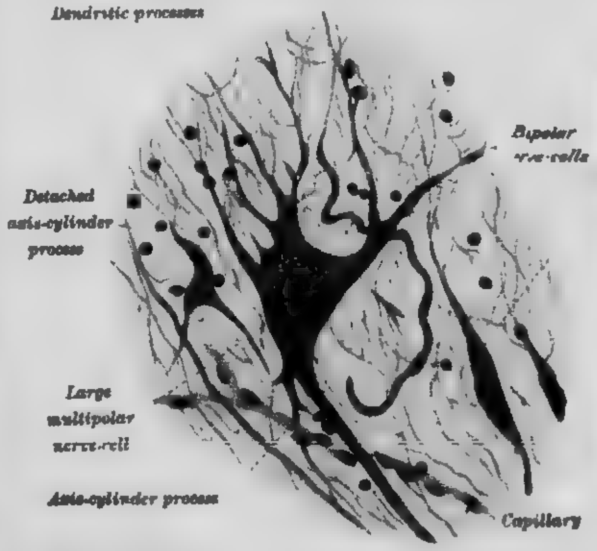


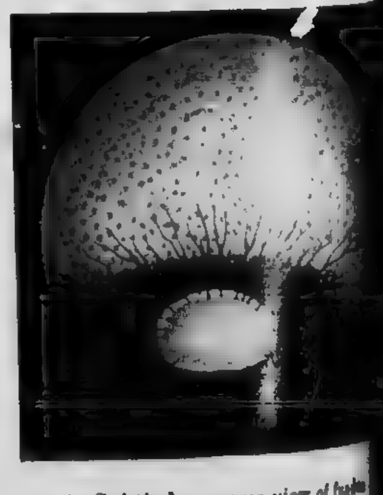
1. Red blood-corpuscles.


Blood of boy, stained with methylene blue solution
Blood of boy Film preparation
Eosin and Löffler's methylene blue
a
b
c
d
e
1
2
3

2. The colourless corpuscles of human blood, × 1000. *a*, eosinophile cells; *b*, finely granular oxyphile cells; *c*, hyaline cells; *d*, lymphocytes; *e*, polymorphonuclear neutrophile cells (Kanthack and Hardy). The magnification is much greater than in 1.

3. Cover-glass preparation of spinal cord of ox, × 250.
(*Stained with methylene blue*).





4. Ophthalmoscopic view of fun
of the horse.

Geo Waterston & Sons, Lith. Edin

illuminated, the tints being a mixture of yellow, green, and blue studded with minute dots; this coloured area is the tapetum (Plate I.). Examination shows this surface to be situated above the optic disc or papilla; the optic papilla appears of a pinkish colour, with a slightly raised whitish margin. It is very difficult to study the eye of the horse, owing to its frequent movement, so that only occasional glimpses of the papilla can be obtained. From the optic papilla a dense network of vessels may be seen radiating but extending no great distance from it; this is characteristic of the retina of the horse. The remainder of the fundus is purple or brown, but owing to its extent very little of it can be seen. In other animals the vessels radiating from the disc are wider apart and more regular, and several of them have received names; moreover, the arteries can be distinguished from the veins, which is not possible in the horse. It is to be borne in mind that the view thus obtained of the fundus of the eye is a magnified image, both the lens and vitreous humour making it appear about three times larger than normal. Owing to the presence of the tapetum in the horse, a perfect examination of the lens and fundus may be made without the aid of artificial light; while under the influence of artificial light

FIG. 102.—DIRECT METHOD OF USING THE OPHTHALMOSCOPE (STEWART).

Light falling on the perforated concave mirror M passes into the observed eye E′; and, both E′ and the observing eye E being supposed emmetropic and unaccommodated, an erect virtual image of the illuminated retina of E′ is seen by E.

the pupil dilates so much that there is no need for the use of atropin.

Accommodation.—All rays of light proceeding from a distant object may be regarded as parallel, and all those proceeding from an object within 20 feet of the eye may be regarded as divergent. A distant object is one situated anywhere between 20 feet from the eye and infinity; an object closer than 20 feet to the eye is called near, and this point increases up to 4 or 5 inches, at which distance no object can any longer be distinctly seen. The nearest distance at which objects can be distinctly seen is called the near point. Parallel rays need no focussing on the retina other than that provided by the cornea; but rays from near objects do require focussing owing to their divergent nature, and it is evident that the nearer the object to the eye the greater the focussing required. This focussing is brought about by a change in the shape of the anterior surface of the lens; it becomes more convex for near objects, and this increase in convexity is due to the ciliary muscle drawing forward the choroid coat, and with it the ciliary processes. By this means the tension normally exercised

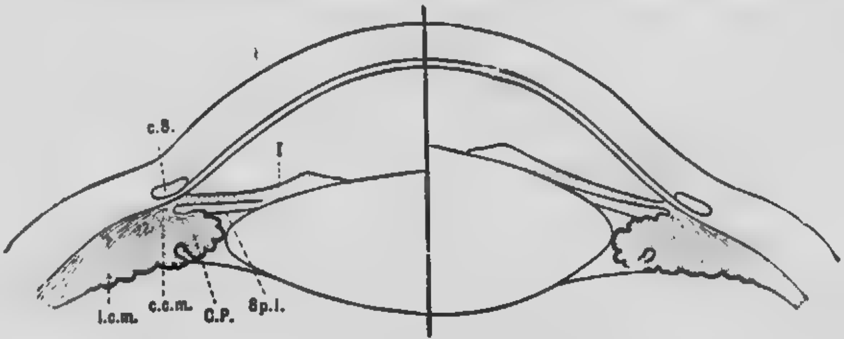


FIG. 108.—DIAGRAM TO ILLUSTRATE ACCOMMODATION (FOSTER AFTER HELMHOLTZ).

C.P. Ciliary process; I, iris; Sp. l., suspensory ligament; l.c.m., longitudinal ciliary muscle; c.c.m., circular ciliary muscle; c.S., canal of Schlemm.

The left half represents the shape of the lens for viewing distant objects, and the right half that for viewing near objects.

through the Zonule of Zinn (the suspensory ligament of the lens) is relaxed, and the lens of its own inherent elasticity bulges forward and so increases the curvature of its anterior face (Fig. 103). A more convex lens is a more convergent one, and its focus is therefore shorter; in this way the images of near objects are brought to a focus on the retina and distinctly seen, whereas if this increase in curvature had not taken place, the image would have been focussed behind the retina. The power the eye possesses of focussing itself is known as the mechanism of accommodation, and the explanation given above is that of Helmholtz; it is the one generally accepted.

When a candle is held opposite to the eye three images of the flame are seen; one a very sharp bright one, obviously reflected from the cornea; a second much duller, but also large, reflected from the anterior surface of the lens; and a third very small, brighter than the middle one, and *inverted*, reflected from the posterior part of the lens (Fig. 104). In a normal eye these are seen perfectly and move in a definite direction when the candle is moved, the inverted image passing in an opposite direction to the two erect images, and all are equally visible at any point on the reflecting surfaces. This phenomenon has been taken advantage of in determining the clearness of the media of the eye, and though superseded by the greater accuracy of the ophthalmoscope, it is still a valuable aid; in cataract one or more of the reflections becomes blurred, and sometimes the image is duplicated.

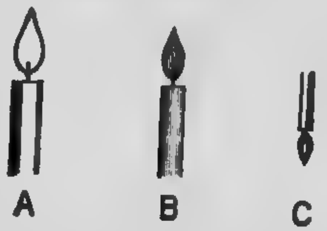


FIG. 104.—DIAGRAM OF THE KATOPTRIC TEST.

A, From the anterior surface of the cornea; B, from the anterior face of the lens; and C, from the posterior face of the lens.

The first and second images are erect inasmuch as they are reflected from a convex surface, but the third image is inverted, being reflected from the posterior surface of the lens which viewed from the front is concave. During the act of accommodation the relative position of these images alters; the second becomes smaller or larger, and advances nearer to or recedes from the first, as the anterior face of the lens becomes more convex or flatter as the case may be. This observation affords the proof that accommodation is due to the varying convexity of the anterior surface of the lens.

Fishes are normally short-sighted, and accommodation for a distant object is effected with them by moving the lens towards the retina.

The ciliary muscle is governed by the ciliary nerves. In the human subject the constrictor fibres of the iris and the ciliary muscle are paralysed by atropin, but in the cat (as first pointed out by Lang and Barrett*), the dog, and certainly in the horse, there is no evidence that any paralysis of the ciliary muscle takes place under atropin, though the pupil dilates. Under the full effect of atropin all these animals can see objects quite close to the eye, and this they could not do if the ciliary muscle were paralysed.

Eyes which possess the power of seeing objects distinctly a few inches from the eye to infinity are known as **Emmetropic** (Fig. 105—1); but all eyes do not possess this range of vision owing to their shape, or more correctly, to the length of the eyeball.

Myopia or short sight is due to the eyeball being too long, whereby the picture is formed in front of the retina, and only a confused and blurred image falls on the retina (Fig. 105—3).

Our observations show that the majority of horses are slightly short-sighted.†

Hypermetropia or long sight is due to the eyeball being too short, whereby, though vision may be perfect for distant objects, those near at hand are not distinctly seen, the picture being brought to a focus behind the retina (Fig. 105—2). It is obvious that a concave glass which scatters rays is the remedy for myopia, while a convex lens which converges them is the appropriate glass for hypermetropia.

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* 'The Refractive Character of the Eyes of Mammalia,' *Royal London Ophthalmic Hospital Reports*, vol. xi., part ii.

† 'The Refractive Character of the Eyes of Horses,' *Proceedings of the Royal Society*, No. 334. 1894.

Fig. 105.—Diagram of an Emmetropic, Hypermetropic and Myopic Eye, to illustrate where the Focal Point exists (Kirke).

In 2 the short eyeball causes the focus to form behind the retina; in 3 the long eyeball causes the rays to come to a focus in front of the retina.

Astigmatism is another error of refraction, due to irregularities in the curvature of the cornea or lens, generally the former. The effect of this condition is that the rays of light passing through one meridian of the eye are brought to a focus earlier or later than those passing through the meridian at right angles to it. The horse is very commonly astigmatic; the horizontal is generally the meridian of least curvature, and corresponds to the long diameter of the pupil.

Errors of Refraction.—In the following table is given the proportion of eyes affected with errors of refraction among 54 horses.

Of 100 eyes (54 horses):
51 were myopic and astigmatic.
2 were hypermetropic and astigmatic.
6 were affected with mixed astigmatism.
39 were affected with myopia.
1 was hypermetropic.
1 was emmetropic.

The amount of error of refraction is as a rule small, the chief visual defect being myopia with or without astigmatism. The number of astigmatic horses is remarkable. According to Lang and Barrett's observations,* the cow would appear to be hypermetropic, and the eye also suffers from astigmatism. In dogs and cats the refraction closely approaches emmetropia. In nearly all the wild animals examined by these observers the refraction was hypermetropic.

The **Movements of the Eyeball** are brought about by means of the ocular muscles; in this way the globe of the eye can be rapidly turned in any direction. But the movements are somewhat complex, for in some of the lower animals, for example the horse, the eyes are laterally placed in the head, so that vision is commonly single-eyed and not binocular as in man. The eye that is viewing an object situated to one side and moving to and fro is being followed in this muscular movement by the eye which does not see; the movements are conjugate, but this only occurs so long as monocular vision is practised. If both eyes be directed to an object situated to the front binocular vision becomes possible, and now the movements are no longer conjugate but opposite, for while the left eye is inclined to the right the right eye is inclined to the left. Another complication in the ocular muscles is due to the movement of the head; it was first pointed out by Lang and Barrett, that in the rabbit and guinea-pig no matter what position the head occupied the pupil was always kept vertical. If the head of the horse or ox be raised or depressed to the fullest possible extent, the muzzle being at one time on the ground, at the next high in the air, it will be found that the eyeballs rotate like a wheel, so that the pupil is still kept horizontal; if it were not for this the pupil in the uplifted head would be vertical and in the depressed head oblique. When the head is elevated the eyeball becomes depressed to such an extent that the sclerotic shows largely above, while the cornea partly disappears beneath, the lower eyelid. When the head is depressed to the ground no more sclerotic shows than when it is in the ordinary position; the probable cause of this will be mentioned presently.

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* *Op. cit.*

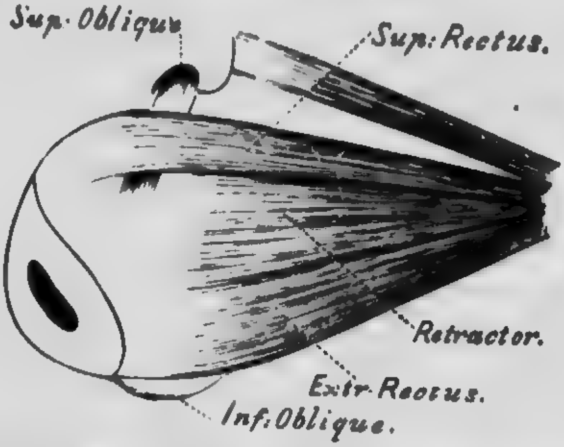

FIG. 106.—THE MUSCLES OF THE LEFT EYEBALL OF THE HORSE VIEWED FROM THE TEMPORAL SIDE.

The muscles of the eyeball (Fig. 106) are seven in number, viz., four *recti*, two *oblique*, and one *retractor*. The use of the recti is clear enough, they rotate the eye in four directions, outwards, inwards, upwards and downwards. The two oblique muscles rotate the eye in opposite directions around its anterior-posterior axis; when the superior oblique contracts it pulls the temporal side of the eyeball upwards, and if it were not counteracted by the inferior oblique it would continue to contract until the pupil became vertical like that of the cat; the inferior oblique pulls the temporal side of the eyeball downwards, in other words these oblique muscles produce a torsion of the globe or swivel rotation, and their action is regulated from the semicircular canals of the internal ear (see p. 502). The retractor partly withdraws the eye in its socket.

The nerves supplying the muscles of the eyeball with motor power are the third pair to all excepting the external rectus and superior oblique, the external rectus being supplied by the sixth pair or abducens, and the superior oblique by the fourth pair or pathetic. So that we have three pairs of cranial nerves supplying seven muscles. The orbicularis palpebrarum, which closes the eyelids, is supplied by the seventh nerve, while the muscle which raises the upper lid derives its nerve supply from the third pair.

The chief movements of the eyeballs are backwards and forwards, corresponding to the directions described as outwards and inwards in man. During these movements it is evident that the external rectus of one eye is acting in conjunction with the internal rectus of its fellow, and such is always the case in monocular vision. Animals with the eyes laterally placed have, however, the power of monocular and also of binocular vision, but the latter is only produced by an internal squint, and the movements of the muscles are now no longer conjugate, for both internal recti are acting together (Fig. 107). Sometimes, then, the group of muscles employed in moving the eyeballs is the same in each eye, at other times it is not. The torsion produced by the superior and inferior oblique muscles is of value in the binocular vision of animals, and in the vertical movements of the head. When the muzzle is raised, as previously described, the superior oblique muscle revolves the eyeball in its socket until the pupil is horizontal; the explanation of the cornea partly disappearing under the lower lid, and the sclerotic showing extensively above, appears to be due to a conjugate action of the inferior rectus muscle whenever the superior oblique is so employed. The inferior oblique is mainly employed with the internal rectus in pulling the eyes inwards for binocular vision, also, as mentioned above, for maintaining the horizontal pupil when the head is depressed or raised.

Monocular and Binocular Vision.—When a horse directs both eyes to the front (Fig. 107) he produces a well-marked double internal squint, and is then capable of binocular vision. The eyes are rotated inwards and slightly upwards by the combined action of the inferior oblique and internal rectus; the pupils are not perfectly horizontal but nearly so, and the pupillary opening is brought so far to the front that the inner segment of the cornea and iris entirely disappear beneath the inner canthus. In no other position than this has the horse binocular vision, viz., single vision resulting from the employment of a pair of eyes, and it is curious to observe that the condition of eye which gives a horse single vision causes in man double vision. Animals with their eyes situated on the lateral side of the head are capable of exercising monocular vision for all objects placed to one side of them and even behind them (Fig. 108);

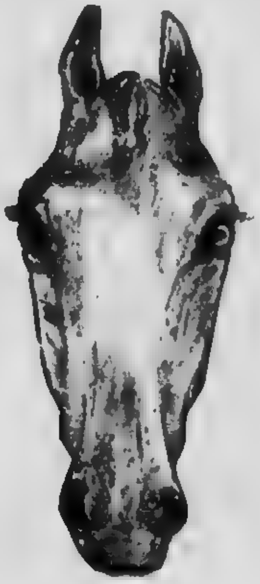

Fig. 107.—The Position of the Head and Eyes in Binocular Vision.

monocular would appear to be for them as perfect as binocular, but on this point it is difficult to judge. It is certain that in the horse when the attention, either from alarm or interest, is *particularly* directed to an object, it is viewed with *both* eyes, the head being held very high, and the ears 'pricked' and turned to the front. In this position it is evident the most sensitive area of the retina is exposed, but there is no *fovea* as in man. A horse can see an object on the ground immediately under his nose, and is able to see when grazing; this is because his face narrows below the eyes. When looking at an object near to him on the ground, he prefers to get his head low down in order to see it; but when looking intently at a distant object, he gets his head as high as possible with the face inclining to the horizontal.

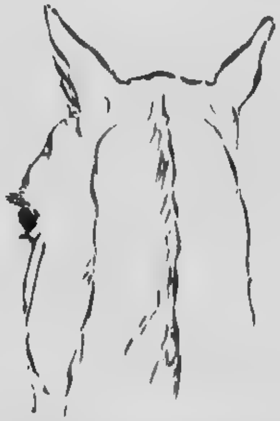

FIG. 108.—DIAGRAM ILLUSTRATING THE EXTENT TO WHICH A HORSE CAN SEE BEHIND HIM.

With the head straight to the front he can see out of the 'tail' of both eyes. By the least inclination of the head, as in Fig. 108, a large visual field behind him may be covered.

Ordinary equine vision is monocular, yet the right eye blinks when an attempt is made to strike the left, though it cannot possibly see what is going on, and in the same way the right pupil contracts when the left is exposed to sunlight. In man binocular vision is perfect, and the explanation afforded is that any part of one retina corresponds to the same part of its fellow; so that if the retinas be laid over one another, the left portion of one will lie exactly over the left portion of the other, and their upper and lower parts will equally correspond; but the

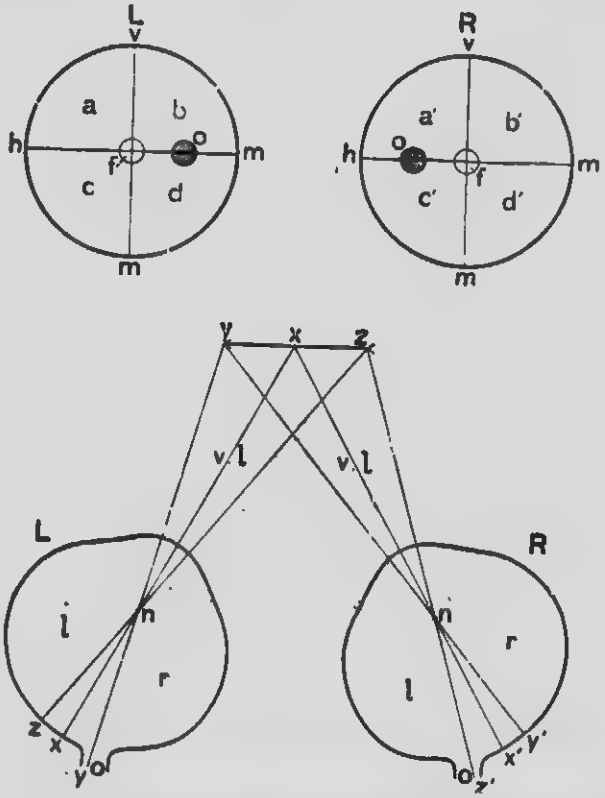

Fig. 109.—Diagram illustrating Corresponding Points in the Human Eye (Foster).

z′ x′ y′ are points in the right eye corresponding to z x y in the left eye; v.l, visual axis. The two figures above illustrate the corresponding points on the retina described in the text.

temporal side of one eye does not correspond to the temporal side of its fellow, but to the nasal side. In Fig. 109, the two circles represent the two retinas divided into quadrants, L being the left and R the right eye; a and c in the left eye correspond to a′ c′ in the right eye, and b and d in the left correspond to b′ and d′ in the right eye; but the optic nerve o is in the left segment of one eye, and the right segment of the other. When the two images of an object fall on corresponding points of the retina of man, vision is binocular and only one object is seen; thus, if the rays fall on the right side of one retina, they must fall on the right side of its fellow. This is shown in Fig. 109, v.l from x to x, and x to x′ are

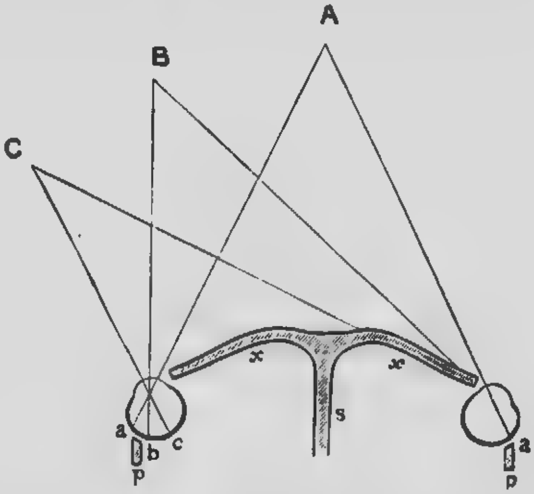

FIG. 110.—DIAGRAM SHOWING HORIZONTAL SECTION OF THE HEAD PASSING THROUGH BOTH EYEBALLS, TO ILLUSTRATE CORRESPONDING POINTS IN THE RETINA OF THE HORSE.

x x, The frontal bones; p p, portion of malar bone entering into the formation of the outer rim of the orbit; s, the nasal septum. Rays of light proceeding from A are seen by both eyes, being imprinted on the temporal side of each retina at a; rays from B are seen at b in the left eye, but are not seen with the right eye; in the same way rays from C are imprinted at c in the left eye, but cannot be seen with the right eye.

the two visual axes; if the object y x z be looked at, z in each case falls to the left of the visual axis, and y to the right, viz., on corresponding points, by which means the object is seen as a single one. Owing, then, to the manner in which the human eyes are placed in the head, and the convergence of axes of the eyeball, a ray of light from any point is imprinted upon the same side of the retina in both eyes, and we see the object not as a double image, but as a single one. This explanation does not apply to the herbivora; no matter how greatly the eyes may be converged in order to see an object, the rays of light do not fall on the same side of the retina, but on *opposite sides* of it. The diagram (Fig. 110) will make this point clear. The outer part or temporal side of the retina in the horse corresponds with the temporal side of the opposite eye; while the nasal side cannot correspond with the nasal side of its fellow, as it is not possible for a ray of light from an object to strike both nasal sides at one time (Fig. 110).

Cartilago Nictitans.—The retractor muscle of the eye withdraws the eyeball within the orbit, and the pressure thus produced within the cavity forces the cartilago nictitans forward, so that it may be made to sweep nearly the whole corneal surface. The reason why the cartilage is pressed forwards is due to the fact that though naturally curved, it becomes flattened and straightened out by the pressure caused by retraction and so shoots forward; when the pressure is removed it retires through its own elasticity, and becomes curved once more.

On the cartilage of some animals is a small gland termed the Harderian; its use is to prepare an unctuous secretion, probably of a protective nature. In the eyelids are found numerous glands, the Meibomian, which furnish an oily secretion, and prevent the overflow of tears.

The **Tears** are secreted by the lachrymal gland which is placed on the upper surface of the eyeball; they find their way into the conjunctival sac by numerous small tubes. The tears pass through the narrow *puncta* into the lachrymal sac, and so into the nostril; once in the sac the descent to the nostril is readily understood, but it is not clear why the tears prefer passing through a narrow slit in the eyelid to running over the side of the face; probably the only explanation is the unctuous secretion mentioned above. The use of the tears is to keep the conjunctiva moist and polished, and to wash away foreign bodies.

The **Eyelashes** of the horse are peculiar. Those on the lower lid are very few and fine, whilst on the upper lid they are abundant, and exist not as a single but as a double row; the rows cross each other like a trellis-work, but without interlacing; these eyelashes are very long and strong (Fig. 111). A few protective hairs grow from the brow and below the lower eyelid, in some horses they are 4 or 5 inches in length; they appear to be in connection with nerve terminations, for their delicacy to the sense of touch is remarkable. The function of these hairs is doubtless protective, and they give the eyes warning of danger.

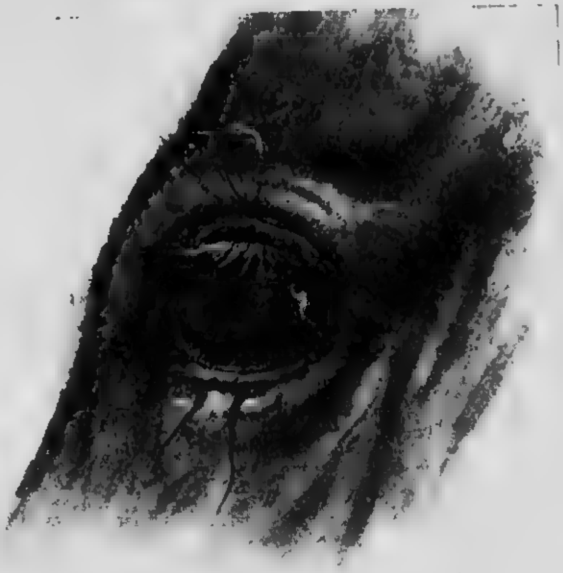

FIG. 111.—THE EYE OF THE HORSE.

Physiological Optics.—When a ray of light enters the eye it has to pass through four surfaces, and including the air four media. There are two surfaces to the cornea, anterior and posterior, and two surfaces to the lens, anterior and posterior; each of these surfaces differs in curvature. As media there are the aqueous and vitreous humours and the crystalline lens; the latter is further complicated by not being of the same refractive index throughout. The formation of an image in such a complex optical system would be difficult to understand, were it not possible to construct theoretically from it a simplified eye, or, as it is known, a *schematic* eye. The basis of its construction is, that so long as a complex system has its surfaces and media 'centred,' that is symmetrically disposed around the optical axis, it is possible to deal with it as if it consisted of two surfaces and two media, viz., the *schematic* eye, and even to simplify it still further to one surface and two media, the *reduced* eye, the media in the latter being air and water. In such a simple optical system it is readily possible to trace the paths taken by the rays of light, and so understand the formation of an image on the retina of the eye.

Cardinal Points.—The most simple optical system which can be devised has an *optic axis* (O A, Fig. 112), viz., a line passing through its centre perpendicular to its refractive surface (a p b); on the optic axis is situated the centre of curvature of the refracting surface, this centre is known as the *nodal point* n. All rays of light which strike the refractive surface perpendicularly, such as O, m′, pass through the nodal point and are not refracted; all rays of light *parallel* to the optic axis, such as c d, strike the refractive surface obliquely and are refracted, and the point where they meet is called the *principal posterior focus*, F_2. On the optic axis, in front of the refractive surface, is situated a point F_1 known as the *principal anterior focus*; rays proceeding from this point strike the surface obliquely, and are so refracted as to be rendered parallel (e f) to the optic axis (O A). To these must be added the *principal point* p, that is the point where the refracting surface cuts the optic axis.

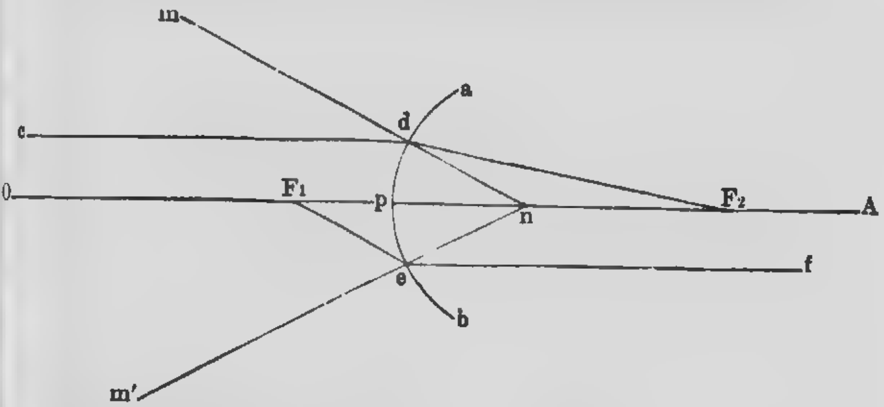

FIG. 112.—THE CARDINAL POINTS OF A SIMPLE OPTICAL SYSTEM (FOSTER).

O A, Optic axis; a p b, a curved spherical surface; n, nodal point; F_2, principal posterior focus; F_1, principal anterior focus; e f, rays proceeding from F_1, rendered parallel to the optic axis; p, the principal point; the rays m d, O p, and m′ e, pass through the nodal point n and undergo no refraction; the rays c d, parallel to the optic axis, are refracted and meet at F_2.

These various points are known as the *cardinal points* of the simple optical system we have imagined. For a more complex system such as the eye, even when simplified, there are two nodal points, two principal foci, and two principal points; but with the reduced eye where we have but one surface and two media, the two nodal points become one, and the two principal points one.

Dioptrics.—In order to be able to calculate the position of the cardinal points of the eye certain data must be known, such as the refractive index of the media, the radius of curvature of each refracting surface, the distance from the cornea to the lens, and the thickness of the latter. A very slight error in the determination of these may produce a considerable error in calculation, so that all measurements made by us on the frozen eyes of horses are rejected as wanting in accuracy, but as an illustration of the measurements of the actual and reduced eye, those furnished by Berlin* are here given, though even

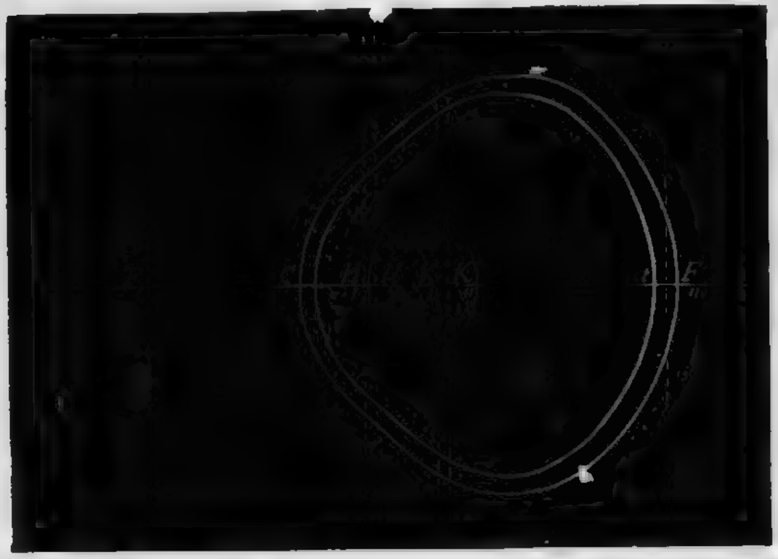

FIG. 113.—THE CARDINAL POINTS OF THE EYE OF THE HORSE (BERLIN).

$F_{\prime}$ is the first principal focus, situate ·7244 inch in front of the cornea.
C is the anterior principal point.
$H_{\prime}$ is the first principal point, distant from the cornea ·3201 inch.
$H_{\prime\prime}$ is the second principal point „ „ „ ·3641 „
$K_{\prime}$ is the first nodal point „ „ „ ·6698 „
$K_{\prime\prime}$ is the second nodal point „ „ „ ·7157 „
$K_{\prime\prime}$ to a is the distance of the retina from the second nodal point. ·8000 inch.
C to $F_{\prime\prime}$ is the distance from the cornea to the second principal focus (which Berlin shows to be behind the retina), 1·7594 inches.

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* *Zeitschrift für Vergleichende Augenheilkunde*, Heft 1, 1882.

these are not free from error. According to Berlin the horse is normally long-sighted, the retina being in front of the second principal focus. What may have been true for the eye he examined is not universally true, for as we have previously stated the majority of horses are slightly short-sighted, therefore the point $F_{,,}$ will fall in front of the retina.

The simplified or reduced eye (Fig. 114), consisting of one surface and two media, gives for the horse, according to Berlin, the following values:

Passage of Light through Lenses.--In nature all rays of light are diverging, but so slight is the divergence of the rays from distant objects, that for the purposes of the eye they are practically regarded as parallel. All rays proceeding from an object situated at from 20 feet to infinity from the front of the eye are considered as *parallel rays*, all rays within 20 feet from the cornea are *diverging rays*. Obviously the nearer the object to the cornea the greater the divergence, so that there is more divergence in the rays proceeding from a body 1 foot from the eye than in one 10 feet from the eye; conversely, the further the object is from the eye the less divergent the rays, until we reach that point beyond 20 feet where the rays may be regarded as parallel.

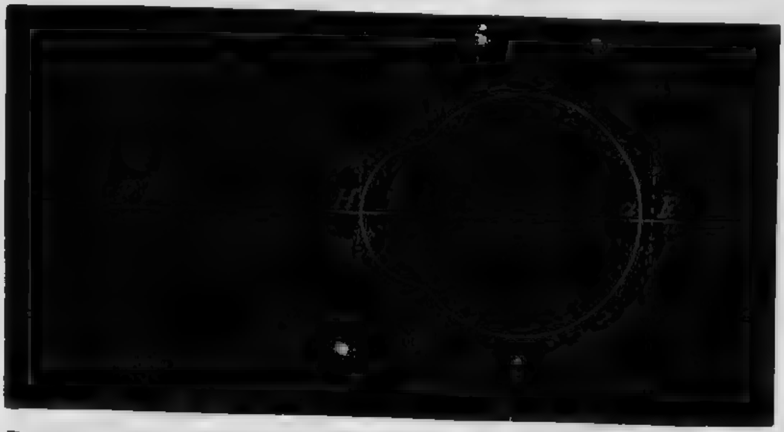

FIG. 114.—THE CARDINAL POINTS OF THE REDUCED EYE OF THE HORSE (BERLIN).

$F_{,}$ the first principal focus is situated 1·068 inches in front of the cornea.
$F_{,,}$ the second principal focus is situated 1·427 inches behind the cornea (in the diagram it falls outside the eye, but this is not normal; see above remarks).
K to *a*, the distance from the nodal point to the retina, 1·004 inches.
H to *a*, the distance from cornea to retina, 1·3683 inches.

A convex lens has two curved surfaces, and a line drawn through the centre of these two surfaces is known as the *principal axis* of the lens (Fig. 115, *m m*). The essential idea of a double convex lens is that it is thicker at the centre than at the edges. Situated on the principal axis of a biconvex lens at a point in its interior is the *optical centre* (Fig. 115, O); any straight line passing through the optical centre is termed a *secondary axis* (Fig. 115, *n n*).

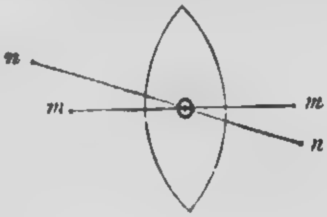

FIG. 115.

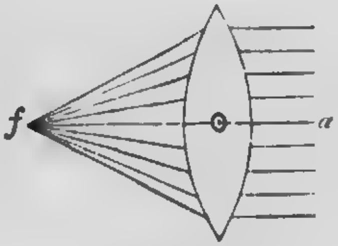

FIG. 116.

FIGURES ILLUSTRATING THE ACTION OF LENSES UPON RAYS OF LIGHT PASSING THROUGH THEM (LANDOIS AND STIRLING).

Fig. 115.—Biconvex lens; O, optical centre; *m m*, chief or principal axis; *n*, *n*, secondary axis.

When *parallel* rays of light (Fig. 116 pass through a convex lens they are refracted and brought to a point *f* on the opposite side of the lens known as the principal focus; the only rays not refracted are those passing through the centre of the lens, viz., those coinciding with the principal or secondary axes. The converse of this is also true, viz., *divergent* rays proceeding from the principal focus of a lens *f* pass through and are rendered parallel (Fig. 116).

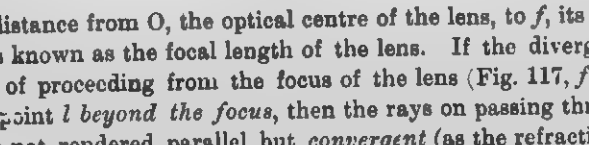

FIG. 117.—Rays of light passing through a convex lens from *l* at a point beyond the focus *f*, cross at some point *v*, and invert the image (Landois and Stirling).

The distance from O, the optical centre of the lens, to *f*, its principal focus, is known as the focal length of the lens. If the divergent rays instead of proceeding from the focus of the lens (Fig. 117, *f*) proceed from a point *l beyond the focus*, then the rays on passing through the lens are not rendered parallel but *convergent* (as the refractive power is more than sufficient to render them parallel), and they come to a focus again on the other side of the lens at the point *v*. The distance from the lens at which they come to a focus depends upon the distance of the luminous point from the lens on the opposite side; thus the nearer the luminous point *l* to the principal focus *f*, the further will the focus on the opposite side recede, and *vice versâ*. The two foci *l* and *v* are termed *conjugate foci*, and as we have shown they have a definite relationship.

If the rays of light proceed from a point L (Fig. 118), which is nearer to the lens than the principal focus F, the lens is unable to refract the rays sufficiently and they issue from the opposite side divergent Fig. 118, *d d*).

Parallel rays of light passing through a *concave* lens, instead of being refracted to a focus are bent so as to become divergent, so that a concave lens has no real focus; but if the divergent rays be produced backwards so as to meet on the principal axis of the lens, the point where they meet is called the *negative focus* of the lens.

FIG. 118.—Rays of light from a point L, between the focus F and the lens, diverge when passing through a convex lens.

Spherical Aberration.—The rays of light passing through a convex lens are not all equally refracted, those passing through the circumference being more bent than those passing near the centre; the result is that the rays do not all meet in the same point, those passing through the circumference of the lens coming to a focus earlier than those passing near the centre. This defect, known as 'spherical aberration,' is remedied in the eye by the introduction of a diaphragm or iris, which prevents some of the rays of light from passing through the circumference of the lens; spherical aberration is further prevented by the fact that the refractive index of the central part of the lens is greater than that of the circumference. Spherical aberration produces indistinctness of vision by the production of circles of diffusion caused by those rays which meet too early crossing each other and forming a circle.

Chromatic Aberration is due to the decomposition of white light

Blue shortest ray
(most bent

into its primary colours by passing through a prism or a convex lens, viz., a spectrum is formed. The colours of the spectrum are differently refracted, the red being the least bent. the violet the most; when therefore we can see the red distinctly the eye is not focussed for the violet. Chromatic aberration is prevented in the eye by the unequal refractive power of the various media, and the action of the diaphragm or iris.

Formation of a Retinal Image.—Rays of light falling on the eye, as from the arrow X O Y (Fig. 119), issue as a pencil of rays from every point of the arrow, the pencil containing a central ray known as the principal ray. All principal rays *a a′* pass through the nodal point *n* without undergoing refraction, while the rays *b c*, and *b′ c′* are refracted to a greater or less extent, so that in this way the retinal image becomes inverted, and very much smaller than the object it represents; it is a miniature though perfect representation of the object presented to the eye. The chief refraction undergone by these rays is at the anterior surface of the cornea; doubtless the other media also refract, the lens for example, but an eye can have very good distant vision without a lens, whose important function is to provide the means for accommodation.

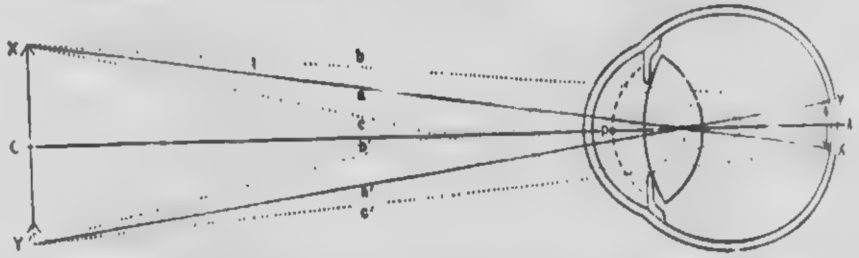

FIG. 119.—DIAGRAM OF THE FORMATION OF A RETINAL IMAGE (FOSTER).

a, Principal ray of the pencil of light proceeding from X; a′, principal ray of the pencil of light proceeding from Y; the principal rays pass through the nodal point *n* without being refracted; the other rays b, c and b′, c′ are refracted. In this way the arrow X Y forms a smaller inverted image of an arrow on the retina Y X.

Theory of Vision.—The change which occurs that enables the vibratory ether to start a nerve impulse by its action on the retina is unknown. A photochemical theory based on the ready decomposition of visual purple has been proposed. In this view it is suggested that the action of light on the visual purple is allied to that of light on the photographic plate, and that the chemical change thus set up in the retina excites a nerve impulse which is transmitted by the optic nerve and tract to the visual centre in the cortex of the brain.

Though the retinal picture is so completely inverted that the right hand of the object becomes the left of the image, and the top becomes the bottom, yet the mind does not perceive the image as inverted, but mentally refers the picture not to the retina but back to the object.

Turning once more to Fig. 119, we observe that the angle X n Y is equal to the angle Y n X. The angle X n Y is spoken of as the *Visual Angle*, and all objects having the same visual angle form the same sized picture on the retina. By the aid of the visual angle the size of an image on the retina may be calculated, provided we know the distance of the nodal point from the retina; thus at the distance of a mile, a man six feet high is represented on the retina of the horse by an image $\frac{1}{540}$ of an inch in height, in the human eye at the same distance the picture of the man would be $\frac{1}{1500}$ of an inch, or about the size of a red blood-corpuscle. The nearer the object the larger the image; taking the six-foot man again at a distance of 10 yards, his height on the retina of the horse would be $\frac{1}{3}$ of an inch, whilst on the retina of a man it would be rather over $\frac{1}{8}$ of an inch.

SECTION II.

Smell.

The nasal chambers are divided by a septum, and each chamber contains the turbinated bones. It has been observed that acuteness of smell is often associated with large and extremely convoluted turbinates. By the arrangement of these bones the nasal passage may be divided into two channels, one which lies next the floor of the chamber, which from its obvious communication leads directly to the respiratory passages, and another channel which lies above it and leads to structures situated very high in the face and nose, but with no outlet save what is furnished it from below. But apart from this there are differences in the physical characters of the mucous membrane which divide the nasal chamber into a lower part through which the air travels, and an upper part which is devoted to the sense of smell; the one is known as the respiratory and the other the olfactory portion. Both the respiratory and olfactory portions of the nasal chambers are supplied with sensation by the fifth pair of nerves.

In the horse the nasal chambers are of extreme importance, inasmuch as it is the only animal we are called upon to deal with which is unable under ordinary circumstances to breathe through the mouth; the majority of animals can breathe through both nose and mouth, but owing to the extreme length of the soft palate in the horse this is under ordinary circumstances impossible. So far as respiration is concerned the question of the nostrils has been dealt with (p. 92), but the arrangement of that portion devoted to the sense of smell has yet to be considered.

From the olfactory tracts in the brain are formed the olfactory lobes, which in some animals possess a well-marked cavity, in others only a canal; in the cavity some fluid is contained which communicates with the cerebro-spinal, and notably in the horse with that contained in the lateral ventricles. From the olfactory bulbs nerve-fibres are given off which penetrate the cribriform plate of the ethmoid, and ramify over the mucous membrane covering the upper portion of the septum, the superior turbinated bone, and the upper third of the superior and middle meatus. The mucous membrane of the olfactory region differs from that of the respiratory portion in being thicker and of a yellowish tint; it is in this membrane that the fibres of the olfactory nerve are distributed. This nerve is non-medullated, and in the surface of the membrane where it terminates two or three different kinds of cells are to be found. One known as a *rod cell* is generally believed to be the terminal cell of the olfactory nerve, though this has also been attributed to a *cylinder cell* which is likewise found in the membrane; other observers consider that both cells are the terminal organs of the olfactory nerve. No definite statement can be made on this point, but perhaps the balance of opinion is in favour of the rod cell being the chief agent whereby odours give rise to nervous impulses which result in smell.

Before an odour can affect the olfactory nerves it has to diffuse into the higher cavities of the nasal chambers, and from being gaseous it must become dissolved in the fluid which bathes these surfaces. We have no idea of the nature of the particles which constitute an odour, but it is certain that before they can make any impression on the olfactory nerve endings, they must become dissolved in the fluid covering the nerve terminations, for a dry olfactory surface is insensible to smell.

There are certain odours which excite the olfactory organs more readily than others; thus flesh, blood, and offal have a remarkably stimulating effect on the carnivora, whilst grass, grain, and vegetable products generally, stimulate the herbivora. The odour of blood or flesh is evidently repulsive to the herbivora, and may even cause nervousness and fright; there are exceptions to this, for we have known a horse eat meat with evident pleasure. Some of the herbivora have a remarkably keen scent, antelopes and deer have the power of detecting the presence of man even a considerable distance away, and it is evident that in most animals the sense of smell plays a more important part in their daily lives than with ourselves. It is through the sense of smell that the male is attracted to the female during the 'œstrous' season, and not only can the odour of a female in this condition be detected at a considerable distance, but the smell is evidently most persistent. The organ of Jacobson, which is well marked in herbivora, is said to have some connection with the sense of smell. Cuvier regarded it as the means by which the herbivora distinguished between poisonous and non-poisonous plants; this is not correct, for cattle-poisoning is comparatively frequent, and in certain parts of the world, for instance, South Africa, is extremely common among horses and cattle. Experience is a valuable factor: animals brought up on a pasturage containing poisonous plants frequently learn to disregard them.

The odour of a body can be detected with greater accuracy by 'sniffing': by this inspiratory act no time is lost in diffusion occurring between the respiratory and the olfactory region, as the odoriferous particles are forcibly drawn upwards. The sense of smell rapidly becomes blunted, at any rate in ourselves: any offensive odour is always most marked when first detected.

By the sense of smell animals have the power of recognising their own offspring; a cow which has lost her calf will yield milk for weeks to a 'dummy' clothed in the skin of the dead calf, and she can recognise the difference between her 'dummy' and that belonging to another cow. If the skin of a young animal, kid for instance, be dressed with an agent which disguises the body smell, the mother is unable to recognise her young. The odour of food is readily recognised by the herbivora, though to the human senses all the grains are equally free from any odour but that of the sack which contains them. Without tasting it, a horse will refuse a grain he is not familiar with. It is possible that everything and everybody has a distinctive odour, at least it would appear to be so from the remarkable manner hounds will follow a scent, or a dog recognise his own master in the dark from amongst a crowd of other persons. In the case of hounds, the amount of odour required to stimulate the olfactory organ must be something too infinitesimal for expression.

Section III.

Taste.

The sense of taste is nearly though not quite dependent upon the sense of smell. There are certain substances which cannot be distinguished when the nose is closed, there are others which can be readily distinguished by the tongue alone. This has led to a classification of taste sensations of which four qualities exist, viz., sweet, bitter, acid, and salt. Animals are certainly capable of distinguishing all of these. It is probable that each distinct taste affects a particular part of the tongue; in man it has been shown that the back part of the tongue is sensitive to bitter tastes, the tip to sweet and saline tastes, the sides to acid tastes, while the middle portion of the tongue is insensitive to any taste. The *flavour* of a substance is not obtained by the sense of taste alone, but by the union of the senses of smell and taste. Without smell taste would be nearly impossible.

On the tongue certain papillæ are found which are intimately connected with the sense of taste, viz., the *filiform*, *fungiform*, and *circumvallate;* the latter are probably the most important in connection with the sense of taste, but the others are most numerous. In both circumvallate and fungiform papillæ, but especially the former, structures are found known as **taste buds**, bulbs, or taste goblets. They are balloon or barrel-shaped bodies, the walls of which are formed of elongated cells resembling the staves of a barrel; this structure is open top and bottom; the nerve fibrils enter below, whilst above is formed the gustatory pore, or opening into the interior of the body of the cell by which fluid finds its way in. Within the goblet or barrel are other cells, processes from which may be projecting at the pore. It appears to be essential to taste that fluid should readily find its way into the pore, and as a provision to ensure this the papillæ containing the buds are situated close to glands. M'Kendrick states that in a single circumvallate papilla of the ox 1,760 taste-goblets have been counted, in the papilla foliata of the sheep and pig 9,500, and in that of the ox as many as 30,000 goblet-cells. The nerve supplying these taste-buds is the glosso-pharyngeal, which is essentially the nerve of taste, and mainly distributed to the posterior part of the tongue; if this nerve be divided the taste-bulbs degenerate. The glosso-pharyngeal nerve consists of a medullated and non-medullated portion; the former terminates in the tongue in end bulbs, whilst the latter proceeds to the taste-goblets. The goblet cells are not strictly limited to the tongue, but have been found in the palate, and close to the epiglottis; they have not been found on the anterior two-thirds of the tongue, a region which we know to be also possessed of the sense of taste, and one not supplied by the glosso-pharyngeal nerve. This area of the tongue is supplied by the gustatory branch of the fifth, and it is to this nerve (which probably receives its taste fibres from the chorda tympani of the seventh) that the sensation of taste is here imparted. Sensation to the tongue is supplied by the lingual branch of the fifth pair, while motor power is furnished by the hypoglossal or twelfth pair.

It is necessary for the purpose of taste that the substance should be dissolved; this is one of the functions of saliva, and experiments on herbivora show that taste produces an abundant secretion from the submaxillary and sublingual glands, though not from the parotid.

SECTION IV.

The Cutaneous Senses and Muscle Sense.

These are *pressure*, *warmth*, *cold* and *pain*, and nerves through which these qualities are conveyed are known in the human subject to be remarkable for the fact that they are distributed in 'spots' throughout the whole cutaneous surface. Whether, as some suppose, there are special nerves which convey these sensations is not definitely known, but it appears to be proved that each of these senses has its own spots of distribution in the skin, those for pain being probably the most superficially seated as well as the most numerous, while the warm spots are the fewest in number and the deepest seated.

Temperature Senses.—Cold spots are more widely distributed than warm, and exist in largest number in the clothed parts of the body. The cold spots are sensitive to cold, the warm spots to warmth; the fact that the former exceed the latter in distribution and number suggests that it is more necessary the body should be made acquainted with the fact that it is cold than that it is hot. In fact the feeling of warmth or cold does not depend upon the temperature of the body but the temperature of the skin. It is obvious that the observations made in the investigation of a temperature sense could only be carried out on man. There is no reason to think it does not equally apply to all animals.

Pressure Sense.—This has also a punctiform distribution, the spots being more numerous than those of the temperature sense. The special nerve endings connected with this sense are found in a ring around the hair follicle, in which position they are obviously most favourably situated for stimulation through the hair itself. In the hairless parts of the skin special tactile corpuscles are found, and in the horse special nerve endings are found in the foot associated with tactile sensibility.

Tactile sensations play a very important part in the lives of animals. In the lips and muzzle, which correspond to the fingers of the biped, are located the touch organs proper (p. 272); the parts are endowed with exquisite sensibility, which enables the animal to be kept acquainted with the nature of its surroundings and the character of its food. The long feelers or hairs growing from the muzzle, face and brow of the horse are in connection with nerves in the skin, and are valuable for tactile and consequently protective purposes. The tactile sensibility of the foot, by informing the animal of the character of the ground it is travelling over, is useful though not absolutely essential in locomotion; nor is the tactile sensibility in the foot of the horse absolutely essential to its safety in progression, as is clearly proved by the results of plantar neurectomy.

Pain Sense is the most widely distributed of the cutaneous senses. It is distributed in spots, probably supplied by special fibres, though no special nerve endings have been determined. Pain confined to the surface of the body can be readily located, but the localisation of interior pain is difficult; that of colic for example is referred to the abdominal wall. It is considered in man that the explanation of the difficulty in localising interior pain is, that the segment of the spinal cord supplying the affected organ, refers the pain to the skin region of the same spinal segment instead of to the organ.

Painful sensations are of various characters, hence such terms as stabbing, boring, burning, throbbing, etc., to express the impression imparted. It is presumed that amongst the lower animals these different qualities of pain exist; it is quite certain, for instance, that the pain exhibited by a horse during an attack of colic is very different from that shown when pus is forming in the foot. Pain may be conveyed by channels which under ordinary conditions convey no sensation, especially is this the case in disease. The normal heart, liver, muscles, bones, etc., may be handled, pinched, wounded, and cauterized, without causing much or any sensation, but under the condition of inflammation they become acutely sensitive, and the same applies to such viscera as the intestines, kidneys, bladder, etc. Of the nature of pain nothing whatever is known.

Muscle Sense.

Sensory nerve endings have been found in muscle and tendon (p. 353). In the former they are spoken of as *neuromuscular spindles;* these from their construction are readily affected by variation in the tension of contracting muscles, and in this way they keep the central organism informed of their condition. They, with the tendon endings, are employed in judging *active* muscular movements; *passive* movements are determined by impulses passing to the centre from the sensory nerve endings in joints, while the *position of the limbs* is known by sensory impressions which arise in the skin and subcutaneous tissue of joints. When muscle sense is lost inco-ordinate muscular contractions occur; well seen in a dog in which the sensory roots leading to the hind limbs are divided. There is, of course, under these conditions, no loss of motor power, yet the animal, through a loss of muscle sense, drags the limbs as if they were paralysed. Later on the sensory impressions which should pass from muscle, joints, and skin, but are unable to reach the cord through the roots being divided, are now replaced by visual impressions, and the dog learns to walk through the medium of his eyes, but if placed in the dark the whole of the pseudo-paralytic symptoms return. From this it is evident that one of the necessary conditions for perfectly controlled muscular movements is a muscle sense pouring in sensory impulses into the central nervous system, and by imparting a continuous knowledge of the condition of the muscles effecting their control.

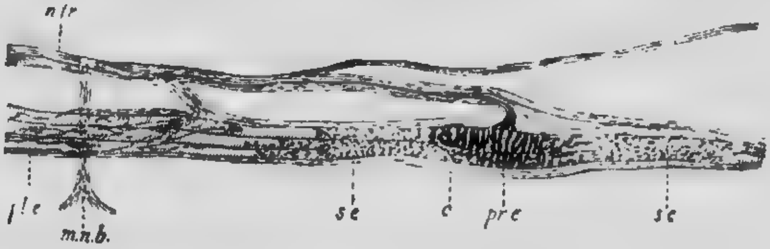

FIG. 120.—MUSCLE SPINDLE (HALLIBURTON, AFTER RUFFINI).

c, Sheath of the spindle; *n.tr.*, trunk of nerve, which sends fibres through the sheath into the spindle, where they form endings (*pr.e.*, *s.e.*, *pl.e.*) of various kinds; *m.n.b.*, bundle of motor fibres (Stewart).

Thirst.

Thirst is referred to the pharynx; observations show that moistening the palate allays thirst, while on the other hand, the filling of the stomach with water through a fistula does not immediately allay the desire for fluid.

The loss of water caused by sweating, purging, etc., is made good to the blood by taking up water from the tissues; in this way the drain on the lymph may be considerable. It has been supposed that the sensation of thirst referred to the palate may be brought about by a deficiency of water or lymph in the part. Little or nothing is known of the nervous apparatus involved in thirst, nor why dryness of the tissues should be referred to the pharynx and palate. The sense of thirst is generally only lost in one particular group of affections—viz., acute disorders of the digestive system in the horse. No horse suffering acute intestinal or stomach pain will, as a rule, drink, yet the dry condition of the mouth suggests that thirst should be present.

Hunger.

Hunger is referred to the stomach. The close approximation of the stomach walls is not necessary for the production in all animals of the sensations of hunger, for some of the herbivora may be very hungry even when the stomach contains a moderate amount of food, the horse and rabbit for example; further, the sensations of hunger may be removed though the walls of the stomach remain in opposition—viz., by the introduction of nutritive enemata. The reason why the sensations of hunger are referred to the stomach wall is unknown.

An animal deprived of its cerebrum shows all the usual signs of hunger, though obviously in this case it is an unconscious exhibition.

Section V.

Hearing.

The Nature of Sound.—When a body is made to vibrate its vibrations are communicated to the adjacent air and give rise in this to waves which travel at a definite rate, and when they reach the ear so act upon its structures as to lead to the sensation of sound. The vibrations which constitute the waves take place to and fro along the direction in which the wave is travelling; in this sound differs from light, whose vibrations are transverse to the direction of propagation.

In comparing one sound with another we are conscious of only three possible differences between them; they may differ in loudness, pitch, and quality. Of these loudness is dependent on the *magnitude* of the to-and-fro motion of the vibrating particles whose movements transmit the sound; a loud sound means a large wave. Pitch, on the other hand, depends on the *frequency* of the vibrations, a high note implying rapid vibrations, or a shorter wave-length.

Sounds may be simple or compound. The vibrations of a tuning-fork give rise to a typically simple sound, of varying loudness or pitch, but possessing little quality. Now, most vibrating bodies do not give rise merely to such simple vibrations, but set up a variable series of different wave-lengths along with their fundamental simple vibration. Thus, most sounds consist of a fundamental tone accompanied by more or less of these other tones—the *partial tones*, *overtones*, or *harmonics*, as they are termed. The quality of a sound depends upon these partial tones; where they are absent the tone is thin, where they are present they give richness, and confer on it that 'character' which enables us to recognise one musical instrument from another by the mere sound it emits.

Those sounds which we group under the general term of 'musical' result from the regularity of their causative vibrations and the definiteness in wave-length of the latter.

Noise is essentially the result of the absence of this regularity and definiteness. We have usually no difficulty in discriminating noise from musical sounds, but the one may merge into the other, as in the case of the noise of street traffic when we are near it, and the musical humming tone it produces when heard from a distance.

From observations on the human subject it has been ascertained that the smallest number of vibrations audible are about thirty per second, while the average human ear can recognise up to 30,000 vibrations per second. It is undoubted that some animals can recognise a smaller number of vibrations than thirty per second. Galton shows that the cat is capable of recognising sounds inaudible to the human ear.

External Ear.—The vibrations of sound are collected by a freely moving funnel-shaped body or external ear; it is composed mainly of cartilage, which is curved and hollowed out in such a way as to form a good collector, while several muscles enable it to assume considerable changes in direction. The two chief directions taken by the ears are backwards and forwards; judging from the behaviour of many horses in carrying one ear backwards and the other forwards, it would appear that they are capable of hearing and appreciating sound in two opposite directions at one and the same time; we say appreciating, inasmuch as something more than mere hearing is required for auditory judgment. The funnel formed by the external ear leads somewhat indirectly to a canal known as the external auditory meatus; in and around this is found an unctuous secretion, and above it, in the funnel of the ear, are many hairs which evidently are for the purpose of protection.

The *movements of the ears* give evidence of what is passing through the mind of an animal. The ears of the horse are turned well to the front and closely pricked—viz., the points approximated, when he is attentive, whether the attention be devoted to a something he is alarmed at or pleased with. The ears are laid back on the poll in sourness of temper and in vice; they are moved rapidly to and fro when a horse is anxious either from impending danger or other cause; one ear carried forward and the other backward or both turned backwards are considered the sign of a good stayer and willing worker, while drooping ears are indicative of muscle fatigue or debility.

Whatever part those remarkables sacs, the **guttural pouches** (confined solely to solipeds), are intended for, it is probable, from their anatomical connection, that they take some share in the sense of hearing, perhaps that of supplying the needful amount of air to the middle ear. The actual use of the guttural pouches is involved in obscurity, but we may provisionally consider them as part of the middle ear. In man acuteness of hearing is enhanced by listening with an open mouth; the fact that the horse cannot breathe through the mouth may explain the presence of these large air-sacs beneath the skull; in other words, they are probably associated with acuteness of hearing.

At one end of the external auditory canal is a piece of membrane stretched completely across it known as the *Tympanum*, it separates the external from the middle ear (Fig. 121). The *Middle Ear* is on the opposite side of the tympanum to the external ear; it consists of a cavity containing a chain of very small bones, known as the *malleus, incus* and *stapes*, which stretch like a bridge across the space from the tympanum to the third or internal ear. The middle, like the external ear, is in communication with the external air, but by means of a passage known as the Eustachian canal which opens into the pharynx. The tympanum has, therefore, air on both sides of it, the object of which is to ensure that the atmospheric pressure on either side is equal, and in this way ensure its free swing. The air finds its way into the Eustachian tube during the act of swallowing, and by the same channel it is conveyed to the guttural pouches.

The *Tympanum* is concave towards the external ear; in the middle ear the handle of the malleus is fixed to the central bulging part of it, and as this bone articulates with the incus, and the latter with the stapes, any alteration in the shape of the drumhead, such as is produced by the vibrations of sound, causes the bridge of bones to move; further, their movement is assisted by some small muscles which are attached to them.

The *Internal Ear*, known as the *labyrinth* (Fig. 122), is composed of the *semicircular canals*, the *vestibule*, and the *cochlea;* these are contained in a solid piece of bone in which two small foramina or windows exist, one known as the *fenestra ovalis*, the other the *fenestra rotunda*; the base of the stapes or third bone of the ear is attached to the membrane which covers the fenestra ovalis.

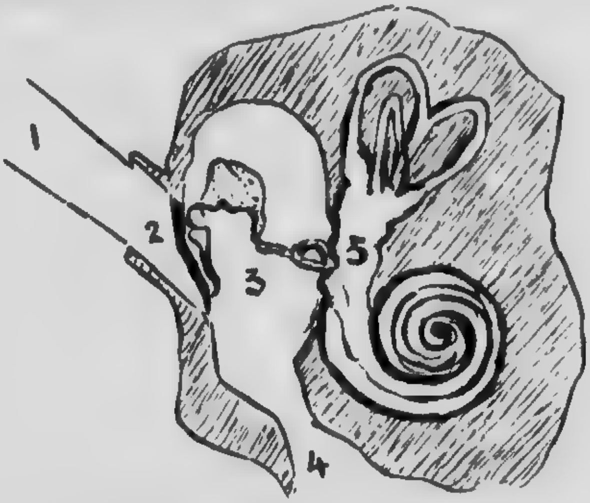

Fig. 121.—Diagrammatic Section of the Horse's Ear.

1, External auditory canal; 2, the tympanum; 3, chain of bones across the middle ear; 4, the Eustachian tube; 5, the internal ear.

All three parts of the *labyrinth* communicate, but it is quite certain that all three do not take an equally active part in hearing. The evidence on this point is clear so far as the semicircular canals are concerned, and some have even included the vestibule, regarding the cochlea as the essential organ of hearing. The whole of the internal ear is lined by a membrane containing a fluid known as the *peri-lymph;* this peri-lymph has free access to all parts of the inner ear.

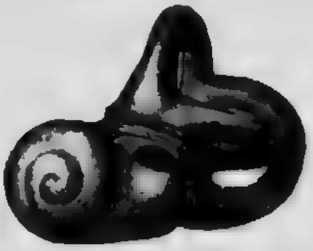

Fig. 122.—The Labyrinth (Edmunds).

The semicircular canals are to the right, the cochlea to the left; both windows may be seen, the *fenestra rotunda* being the lowermost. The groove across the body of the organ lodges the auditory nerve. The figure is enlarged.

Within this membrane is a membranous labyrinth, the counterpart of the semicircular canals and vestibule, and this also contains fluid known as *endo-lymph*. The membranous labyrinth is composed of two pouches, the *saccule* and *utricle* lying in the vestibule; with the latter the membranous semicircular canals are connected, while the former communicates with the middle canal of the cochlea. On both utricle and saccule is an area known as the macula acustica, on which branches of the auditory nerve are distributed to cells known as hair cells; similar areas exist in the semicircular canals. The hairs on the cells project into a mucoid mass frequently containing crystals of carbonate of lime; these crystals are known as *otoliths*.

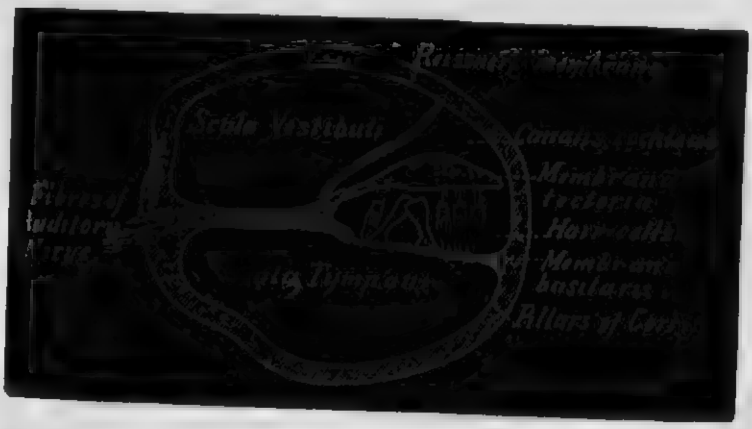

FIG. 123.—DIAGRAMMATIC TRANSVERSE SECTION OF A TURN OF THE COCHLEA (STEWART).

The two windows existing in the bony labyrinth have been mentioned above. The base of the stapes lies over one of them, and between the stapes and the peri-lymph is the membrane which lines the internal ear. Every movement of the tympanum causes the bony bridge to oscillate, and every oscillation of this thrusts the stapes against the membranous window, and so sets up oscillations in the peri-lymph which are transmitted throughout the internal ear.

The *cochlea* resembles in appearance the shell of a snail, its interior being divided into three spiral channels which wind their way from base to apex like a circular staircase. The number of twists in the cochlea is two and a half; the axis around which these wind is composed of soft bone, having canals up which the auditory nerve travels. If a spiral of the cochlea be cut across (Fig. 123) the three canals it contains are seen. These are divided by septa; one septum, known as the *lamina spiralis*, separates the upper canal or *scala vestibuli*, from the lower one or *scala tympani*. The third, or middle canal, is of a triangular shape and called the *cochlear canal;* it contains the essential organs of hearing, and lies between and to the outside of the other two. The roof of the cochlear canal is formed by a piece of tissue known as the *membrane of Reissner*, whilst its floor, on which is situated the essential organs of hearing, or *Organ of Corti*, is formed by the *membrana basilaris*, which connects the outer wall of the cochlea to the lamina spiralis. The cochlear canal is the continuation of the membranous labyrinth. The upper passage of the cochlea, viz., the scala vestibuli, is continuous with the lymphatic peri-lymph space of the vestibule, whilst the scala tympani, or lower passage, ends at the base of the cochlea in a blind extremity in which is a membranous window, the fenestra rotunda, which separates the scala tympani from the cavity of the tympanum. The cochlear canal terminates suddenly at the summit of the cochlea, and at this point the two scalæ, which in their windings have been decreasing in size from base to apex, meet and communicate by a small opening, the *helicotrema*, and the fluid of the one is thus in connection with that of the other.

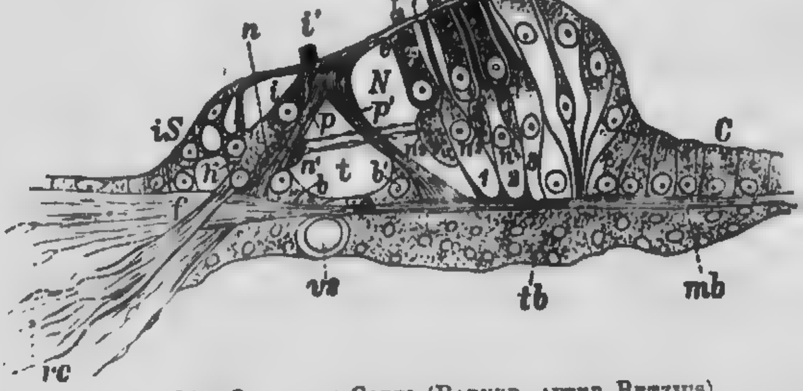

FIG. 124.—ORGAN OF CORTI (BARKER, AFTER RETZIUS).

mb, Basilar membrane; *rc*, nerve fibres passing in to arborize around the hair cells; *p*, inner pillar of Corti, with its basal cell, *b*; *p'*, outer pillar, with its basal cell, *b'*; 1, 2, 3, supporting cells of Deiters; *H*, Hensen's supporting cells; *i*, internal hair cells with its hairs; *e*, external hair cells; *e'*, hairs of three external hair cells; *n*, n^1, to n^4, cross-sections of the spiral strand of cochlear nerve fibres (Stewart).

Organ of Corti. — This consists of a triangular-shaped tunnel (Fig. 124), the base of which rests on the basilar membrane; the tunnel is composed of certain rods arranged side by side, inclined from both sides towards each other and meeting superiorly like an inverted V. At this point the rods, known as the rods of Corti, fit into each other in a peculiar manner. Flanking either side of the tunnel are certain cells of two distinct kinds; those nearest to the tunnel are somewhat flask-shaped, and having hairs growing from their summit, are spoken of as the *inner* and *outer hair cells*; external to the outer hair cells are some tall conical cells known as *Hensen's cells*. It will be remembered that the auditory nerve ascends the axis of the cochlea, giving off fibres which in their passage ramify over the lamina spiralis, at the outer edge of which the above-described organ of Corti exists; having reached this the fibres lose their medulla, and the naked axis cylinders pass into the cells flanking the triangular tunnel, some fibres crossing the tunnel to reach the cells on the opposite side. How the nerve terminates in the hair cells—for it is to these that it is distributed—is unknown, but that the hair cells are the organs of hearing is undoubted; Hensen's cells are probably only of a nutritive nature and unconnected with auditory impulses. This description of the organ of Corti is as it presents itself in tranverse section; if, however, we look at the tunnel from above where the rods from either side meet, it is observed that in their union the rods of the outer wall of the tunnel fit into the heads of the rods of the inner wall, and the squareness of their heads is such that the arrangement is very like the keyboard of a piano.

Auditory Sensations.—Any analysis of these is hardly necessary in a work dealing with the lower animals; we have no direct evidence that they understand or appreciate the difference between music and noise; a dog will howl at one as readily as another. At the same time it is certain that animals can learn to recognise sounds and associate them with certain ideas, as for instance the commotion and excitement amongst the horses of a regiment when the trumpet sounds 'feed,' and again the recognition by a dog of its master's voice. Further, we have undoubted evidence that sounds which are so feeble as not to affect the human ear are readily perceived by some animals, so that the acuteness of their sensations is greater than that of our own, though their capacity for the enjoyment of music is absent or extremely small.

The vibrations set up in the tympanum are, as we have seen, communicated to the chain of bones, the stapes of which, through the fenestra ovalis, imparts a push to the peri-lymph of the labyrinth; this fluid transmits the impulse through the vestibule, and from here into the scala vestibuli of the cochlea. The vibrations ascend the spiral staircase, and set in motion the membrane of Reissner, which causes the lymph in the cochlear canal to vibrate; when these vibrations reach the summit of the cochlea they enter the scala tympani through the helicotrema. The lymph in this canal is now set in motion, with the result that the basilar membrane, on which the organ of Corti rests, is affected, and the vibrations are ultimately lost at the blind extremity of the canal, whose membrane is pushed outwards at the fenestra rotunda. Every push inwards at the fenestra ovalis causes, therefore, a push outwards at the fenestra rotunda. During the time the vibrations are crossing the cochlear canal from one scala to another the organ of Corti is affected, and by means of the auditory nerve the impulse is conveyed to the brain. It is in this organ of Corti, with its nerve endings, that the complex sounds which make up even a single note of music are analysed, and this analysis was at one time supposed to be effected by the rods of the organ, which were believed to vibrate to their own particular tone, in the same way as a tuning-fork will pick out its own tone from sounds in its vicinity and vibrate to it. This view, tempting as it is, is negatived by the fact that the rods of Corti do not exist in birds, and it has therefore been supposed that the vibrations to the nerves terminating in the organ are set up by the vibration of the basilar membrane on which the organ is built, but the question is far from settled.

Even the function of the vestibule is disputed; while some hold from analogy that it is connected with auditory sensations—through the nerves terminating in hair-cells which are found on the areas previously described as the macula acustica—others believe that it is wholly devoted to the perception of movements of the body, by which means the animal is informed of the extent and direction of its own movements.

The **Semicircular Canals and Labyrinth**, though connected with the internal ear and sharing in common with it the nerve of hearing, are yet devoted to functions of quite another kind. To the labyrinth is assigned the control of the ocular muscles and the maintenance of the horizontal position of the pupil (see p. 472). It is also engaged in the obscure problem of muscle tonus (p. 364), and this is gathered from the fact that destruction of it delays the appearance of rigor mortis on the same side. Finally, the labyrinth is the means by which the body learns, or is made acquainted with its position and movements, and this is effected by impulses proceeding from it to the cerebellum. To quote the words of Sherrington, the labyrinth keeps the world right side up for the organism, by keeping the organism right side up to the external world. This function falls to the semicircular canals, the arrangement of which is peculiar and interesting.

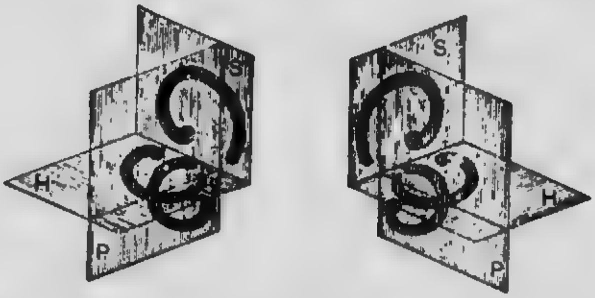

FIG. 125.—DIAGRAM SHOWING THE POSITION OCCUPIED BY THE SEMICIRCULAR CANALS. AFTER EWALD (STEWART).

H, P, S, are three mutually rectangular planes which indicate the position of the canals. In the horizontal plane, H, are found both *external* canals; in a vertical longitudinal plane, S, are found both *superior* canals; in a vertical transverse plane, P, both *posterior* canals are placed. The plane of the superior vertical canal of one side is parallel to the plane of the posterior vertical canal of the opposite side.

There are three bony semicircular canals, so arranged that their three planes are placed at right angles to each other, two being vertical and one horizontal (Fig. 125); within each bony canal is one of membrane, the two being separated by a fluid known as the peri-lymph. Within the membranous canals is also a fluid known as the endo-lymph, and at certain parts of the canals the vestibular branch of the auditory nerve has special nerve endings known as hair-cells. Impulses set up in these hair-cells are brought about either by alterations in the pressure of the peri-lymph, such as occur in consequence of movement, or by mechanical stimulation produced by grains of calcium carbonate (otoliths) found in the labyrinth, closely associated with the nerve endings. Impulses so set up are conveyed to the cerebellum, which is the centre dominating the co-ordination of muscular movements, and the movements necessary for equilibration.

The semicircular canals are arranged as above described, so that movements of the body in the three dimensions of space may produce their respective effects on the brain. It is by means of them that an animal is made acquainted with the direction in which its body is travelling, forward or backward, right or left, up hill or down, or in the movements which occur in jumping. It is no wonder, considering their extraordinary importance, that these canals are securely lodged within the substance of the hardest bone in the body.

If the semicircular canals be injured the resulting phenomena depend upon the position of the canal which has been destroyed. If the horizontal canal, the head oscillates in a horizontal plane; if the vertical canals be damaged forced movements occur in a vertical plane; standing and locomotion become impossible. If all three canals are destroyed violent inco-ordinate movements result, the animal turns somersaults, the head is twisted, the eyeballs roll from side to side, and special measures have to be taken to prevent the creature killing itself through its own violence.

CHAPTER XVI

THE LOCOMOTOR APPARATUS

The muscles are attached to bones, and these, by their movements, may be inclined to each other at angles of varying size. These angles are opened and closed during progression, and the mechanical aid which is introduced to effect this is that of the lever. The **Lever** is composed of a power, fulcrum, and weight, and according to the relative positions which these occupy, a lever is spoken of as being of the first, second, or third order.

In a *lever of the first order* the power is at one end, the weight at the other, and the fulcrum between the two. The muscles which extend the head act as a lever of this order, the head being the weight, the occipito-atloid articulation the fulcrum, and the muscles of the neck the power. In extension of the hind-leg the gastrocnemii muscles are the power, the hock-joint the fulcrum, and the leg below the hock the weight. A lever of the first order is principally a lever of extension, and exists all over the body; it is also a lever of power, for if the long-arm be 5 feet, and the short-arm 1 foot, a power of 1 lb. at the long-arm will support a weight of 5 lbs. on the short-arm. It is to be noted that as a lever increases in power it loses in speediness of action.

In the *lever of the second order*, which is a rare one in the body, the weight is placed between the fulcrum and the power as in a wheelbarrow, the wheel being the fulcrum. When the leg is fixed on the ground and the body passing over it a lever of the second order is formed, the ground being the fulcrum, the triceps or gastrocnemii the power, and the body through the elbow or hock joints the weight.

The *third order of lever* is the lever of flexion. The power is placed between the fulcrum and weight; the nearer the power is to the fulcrum, the greater the flexion obtained for a given expenditure of muscular force. This lever is one for speed, and what it gains in speed it loses in power; it is therefore a wasteful lever, but an essential one in the limbs. Examples of it in the body are numerous; in the flexion of the elbow-joint, the weight is the leg below the elbow, the power is the flexor brachii muscle at its insertion into the radius, whilst the elbow-joint forms the fulcrum. In the flexion of the hock the power is the flexor metatarsi, the fulcrum is the hock-joint, the weight being represented by the limb below the hock. The reason why the third lever is more frequent than the others, is due to the fact that the chief movements of the limbs are directed to moving comparatively light weights through a great distance, or through a certain distance with great precision, rather than moving heavy weights through a short distance (Foster). As to the weight to be carried, we may say that the weight of the fore-leg of a cavalry horse cut off at the elbow was found to be 17 lbs. 8 ozs.; cut off at the knee, through the upper row of bones, it was found to weigh 7 lbs. 10 ozs.; one fore-foot with corona weighed 2 lbs. 3 ozs., and the hind-leg, cut off at the hock-joint, weighed 10 lbs. 9 ozs.

Stillman* points out that the terms flexor, extensor, adductor, and abductor, cause the chief function in muscles to be lost sight of, viz., the power of propelling; it is necessary, however, to remember that propelling is not a power apart from flexion and extension, but the result of them.

Co-operative Antagonism.—As a rule, to which there are certain exceptions, the contraction of any group of muscles is attended by a contraction and not a relaxation of their antagonists. This is described by Waller as 'Co-operative

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* 'The Horse in Motion.'

Antagonism.' The amount of contraction thus exhibited by antagonistic muscles is insufficient to neutralize the effect of the direct motors, but it would appear that for the due performance of such movements as flexion, extension, etc., the antagonistic group of muscles should offer some slight opposition. This can readily be demonstrated by flexing the fingers and grasping the arm with the opposite hand; both extensor and flexor muscles will be felt to harden. Moreover the opposition of antagonistic muscles appears in many cases to be essential to the due performance of movement; Waller quotes as an example of this the fact that in lead palsy only the extensor muscles of the arm are affected, yet the flexors are powerless to act.

The difference existing between the articulation of the fore and hind limbs with the trunk has until recent years been the cause of considerable error being promulgated. It was previously supposed that the muscular attachment of the fore-leg to the trunk indicated that the body was simply slung between the fore-legs, the latter acting as props whilst the hind-limbs did the work. Instantaneous photography has shown us that the fore-limbs not only act as props but as propellers of the body; especially is this seen in the gallop, where by measurement it has been shown that one fore-leg will propel the body a distance of 10 feet, and in so doing will raise it 4 inches in height in a vertical direction.* By means of the fore-legs also, the horse is enabled in draught to assist its hind-legs in stopping weights.

Joints are formed wherever two bones come into contact. Dealing only with those joints in the limbs which are of the most practical interest, it is observed that ball-and-socket joints (as in the hip), hinge-like joints (as in the hock), and gliding joints (as in the knee), are found; all these are coated with articular cartilage and lubricated with *synovia*. Synovia is a viscid, yellow, alkaline fluid containing proteids, mucin, and salts. The viscidity of synovia is due entirely to the mucin it contains, and this confers on it its slippery nature. There is no difference between the synovia of joints and that of bursæ. It is said that the amount of synovia in a joint is greater in animals at rest than in those at work, but the extra bulk appears to be due to an increase in the watery material, whilst the proteids are decreased; the salts, on the other hand, especially those of sodium, exist in a larger proportion than in the synovia of working animals.

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* Stillman, 'The Horse in Motion.'

The bursæ in the limbs of the horse are very important structures; they are placed where the tendons pass through bony channels, and without them the rapid movements of the limbs would be impossible; that the strain on them from wear and tear is considerable we know from practical experience.

Hock-joint.—Solipeds appear to stand alone in having the ridges of the astragalus placed obliquely, instead of vertically as in other animals; the oblique ridges in the horse occasion some considerable difference in the action of the limb. It is usual to speak of a screw action of the hock produced by the oblique ridges of the astragalus; this screw action, we believe, is an entire misconception. The ridges on the astragalus do act as a screw but not on the hock; *the effect is on the stifle,* and produces that remarkable stifle action particularly well seen in trotters. If the ridges on the astragalus turned the hock outwards, every horse would travel as if it were 'cow-hocked.' The leg below the astragalus is carried directly forwards; when, however, it comes to the ground, and the body passes over it, it is not uncommon in some horses to observe a considerable twist *outwards* of the hock-joint, the toe being turned in; this is due to the *ascent* of the lower end of the tibia on the astragalus, leading to the upper end of the tibia *turning in the stifle-joint,* the result of the leg being extended. The object of the stifle being turned outwards during the flexion of the leg is to clear the abdominal wall, and the reason why solipeds have oblique ridges on the astragalus and ruminants and carnivora vertical ones, is that the ribs of the latter class are short and do not come near the pelvis (as in the horse), and therefore the abdominal wall is not in the way. A spring or automatic flexion action in the hock has been described, such as may readily be observed in the dead leg, when if the hock be flexed slightly it either flies back or completes its revolution with a jerk. This condition does not exist during life, nor after death until rigor mortis occurs; it is produced by the lateral ligaments of the hock-joint, and is purely a post-mortem condition.

The flexor metatarsi muscle is remarkable in having a tendon running its whole length, so that from the origin at the femur to the insertion at the front of the hock there is a stout tendinous cord. A somewhat similar arrangement exists in connection with the gastrocnemii muscles. When the flexor metatarsi acts the hock is flexed, but the use of the tendon running from origin to insertion is not at first sight quite clear. Chauveau considers that it automatically flexes the hock, but tendons are devoid of any such power; it would appear that its function is to relieve the muscle when the animal is standing, or sleeps standing. When muscles which perform flexion and extension are acting together with equal force no movement results; such is the case when the weight is on the limbs and the animal at rest. When a horse is at rest his gastrocnemii muscles and flexor metatarsi are acting in opposite directions and equally; the one is trying to close the femoro-tibial angle, the other keeping it open. It is the function of the tendinous portion of the flexor metatarsi and gastrocnemii muscles to assist in keeping the leg fixed without any great muscular effort.

The chief movement of the hock occurs between the tibia and astragalus. Though the range of motion between these bones is considerable, yet it is not fully exercised in all paces; it is only in the jump and gallop that the angle formed between the tibia and metatarsal is closed to any great degree. When the joint is completely flexed in the dead dissected limb, if we look at the posterior part, viz., the now uncovered ridges of the astragalus, we find that when the joint is flexed to the utmost the *tibia and* *astragalus are no longer in apposition*, the tibia has partly left the astragalus and a small space exists between them. To prevent flexion to a dangerous degree two stops are placed on the anterior face of the inferior extremity of the tibia, one outside, the other inside, the outside being the larger of the two; these stops come into contact with two rests on the astragalus, and in this way we think a certain amount of jar may be imparted to this bone. As the inside stop comes into contact with the astragalus slightly before the outside stop, we conceive it possible that the inside of the astragalus receives more concussion than the outside. Can this help to offer any explanation of the position of spavin? Of the ridges on the astragalus, one is narrow, the other broad; the narrow one is the inside ridge, and it runs completely down to the surface which articulates with the magnum, and sometimes considerably overlaps it.

The movement in the true hock-joint is very simple as well as extensive; but the movements between the small bones composing the joints are complicated. In the first instance they are very limited; the astragalus moves on the magnum, the magnum on the medium, and the medium on the large metatarsal; but the amount of movement in these is not the same, the movement between the astragalus and magnum being the greatest. One might suppose that the movement in this part was rather of a front to rear, viz., to and fro character, though the fact that the ligamentous attachment between the bones is situated at the central part suggests that this is probably not the case. Pathology proves the correctness of the latter supposition. An examination of the face of these bones when affected with articular disease exhibits well-marked, sharp, and rather deep grooves, which run *obliquely* across the surface of the bones, and are better seen between the astragalus and magnum than elsewhere. The grooves are the result of friction during the movement of the joint, and they indicate that the motion of these bones on one another is more of the nature of a rotation. Again, these grooves show where the greatest amount of pressure normally comes on the bones; it will always be found that the most extensive damage in disease is on the anterior and internal surface, and this rule holds good whether it be the astragalus, magnum, medium, or head of the large metatarsal which we are examining. If a longitudinal section of the leg from the thigh to the fetlock be made, it is observed that the line of weight on the bony column mainly falls through the anterior part of the hock-joint. There can be no doubt that this pressure is removed by resting the leg, viz., flexing the hock, and this is probably the reason why no horse ever stands for any length of time resting equally on both hind-legs.

The **Stifle** is the largest joint in the body; the cause of its rotation has been previously described. One function of this joint is that of rendering the limb firm and rigid when the foot is on the ground, and this it does by the contraction of the muscles inserted into the patella; if the latter bone be kept fixed on the upper part of the trochlea of the femur, no flexing of the hock or stifle can occur. This experiment can be readily tried on a horse just destroyed; the limb having been extended, the simple pressure of the hand on the crural muscles is sufficient to prevent the bending of the hock unless considerable force be employed. No bending of the hock during life can occur if the foot be kept extended; the first movement in the advance of the leg and the flexing of the hock and stifle is that the foot is flexed. In a certain surgical condition, commonly known as dislocation of the patella, the limb is rigid from the femur to the metatarsus; but, though the foot may be flexed, neither hock nor stifle responds, owing to the patella being fixed. We believe that in the majority of these cases the patella is not fixed from dislocation, but from cramp of the vasti muscles. The amount of movement in the stifle is considerable, and to admit of it being carried out with perfect freedom, the convex condyles of the femur play in cups formed of cartilage on the upper surface of the tibia.

The **Hip** is a cup and ball joint; the range of outward movement obtained by it in the horse is limited by the insertion of the ligamentum teres (and pubio-femoral ligament) into the inner side of the head of the femur, and not into its centre as in most other animals. This is said to be the reason why the horse rarely 'cow-kicks.' The lengthening of these ligaments accounts for 'cow-hocks' in horses.

The **Shoulder-joint** is characterized by the considerable surface of movement afforded by the humerus and the small surface of the scapula, the object being to obtain a large range of motion for the humerus.

The **Elbow** presents an articulation with ridges which influence the turning outwards of the knee in progression; if the knees are turned out too much the leg below is thrown in as it is brought forward, and in this way one cause of 'brushing' and 'speedy cutting' is produced.

The **Knee** consists of three main joints and numerous minor ones; the upper joint possesses the largest range of motion, whilst the lower joint practically does not open. Probably such defects as 'speedy cutting' and its opposite condition, 'dishing,' are influenced not only by the elbow, but by the shape of the articular surfaces between the radius and upper row of bones. The radius is peculiar in presenting on that articular surface next the knee a concave surface anteriorly and a convex one posteriorly; these form two condyles, of which the inner is more curved than the outer. The outer condyle plays on the trapezium, cuneiform, and lunar; the inner condyle plays solely on the scaphoid. When the knee is flexed the influence of the condyles is seen; the concave articular surface of the radius is removed from the surface of the bones of the knee, and the convex articular surface appears as the joint grows wider. The inner condyle being larger than the outer depresses the scaphoid, so that a very important movement occurs between the scaphoid and lunar. This action of the radius on the scaphoid throws the foot slightly outwards, probably with the object of enabling it to clear the opposite limb. We believe that an examination of the knees of 'dishing' horses will show that extreme curvature of the inner condyle of the radius is the cause of the action, in the same way that turned-in elbows, and alterations in the curvatures of the radius and humerus, will probably account for horses throwing the foot inwards, and thus 'brushing' or 'speedy cutting.'

The **Fetlock Joint**, owing to the presence of the sesamoid bones, forms a yielding articulation. In a state of repose the greater part of the horse's weight is borne on the posterior half of the metacarpal articulation and the articular surface of the sesamoids. One great advantage gained by the articulation of the fetlock being yielding is the destruction of the concussion of impact when the body comes to the ground. A similar condition is observed in the joint of the foot, for which see the chapter devoted to that subject.

The **Function of the Suspensory Ligament** has been a fruitful source of discussion. Its chief use, no doubt, is to support the fetlock; in no other way could a joint be supported which is placed in this part of the limb, possessed of so much motion, and exposed to such concussion. Though ligaments and tendons are held to be non-elastic, yet we must claim for the suspensory ligament a little more elasticity than would be obtained if the sesamoids were united by bony tissue to the metacarpal, and the pleasantness and freedom from jar experienced in the riding-horse are in part due to the suspensory ligaments.

Stillman claims for the suspensory ligament a function which he believes to be demonstrated by instantaneous photography, viz., that it acts the part of a spring, flexing the fetlock sharply when the weight is taken off it, and explains why the dirt is thrown out of the feet of a galloping horse. We have no evidence of the correctness of this statement; the sharp picking up of the foot from the ground in walking (a movement so rapid as almost to defy detection) must rest with the flexor muscles. Besides these functions, the suspensory ligaments assist the horse to stand while sleeping. If the suspensory ligament be divided, the fetlock sinks but does not come to the ground; if the perforans be divided a slight sinking of the fetlock is the only change. To bring the fetlock to the ground, both flexors and suspensory ligament must be divided, which demonstrates that all three support the weight while standing.

Function of the Check Ligaments.—Horses are enabled to sleep while standing, and remain for some considerable time without lying down, by means of a singular arrangement of so-called 'check' ligaments which exists in both fore and hind limbs; we have previously touched on this question so far as the hind-limb is concerned. The flexor tendons of the fore-limb support the weight, the extensors keep the limb rigid. In order that the strain of supporting the weight may not be placed solely on the muscles of the arm, both flexor and extensor tendons receive branches of ligament from the radius and metacarpus. These are attached to the tendons in such a way as to cut off the muscles, at any rate, to a considerable extent, from the strain of standing in one position for any length of time. In the act of standing the rigidity of the bony column of the leg is maintained by the extensor tendons, each phalanx having an extensor attached to it, viz., the extensor metacarpi leading to the large metacarpal bone, extensor pedis to the corona and pedis (receiving also a slip from the suspensory ligament), and extensor suffraginis to the suffraginis. This latter receives a strong slip of ligament from the outside of the carpus, which entirely takes off the strain from the muscle, and keeps the tendon taut during sleep. Further, the horse is enabled to stand whilst sleeping by means of the fascia of the arm and thigh; both of these are attached to the muscles and tendons of the part, affording them considerable support of a non-muscular nature.

Centre of Gravity.—The centre of gravity at rest is fixed, but during motion it oscillates from front to rear, depending on the position of the body and the pace. Owing to the fact that more weight is carried on the fore than on the hind legs, the centre of gravity lies nearer to the elbow than the stifle. If a vertical line be dropped just behind the ensiform cartilage of the sternum, and intersected by a horizontal one passing through the lower part of the middle third of the body, the point of intersection is the centre of gravity of the body at rest; this is the rule given by Colin. We may say, speaking roughly, that the vertical line passes about 6 inches behind the elbow, the horizontal just below the shoulder-joint; the centre of gravity is where these intersect. It is obvious that the position of the centre of gravity will vary with different horses, but not to such an extent as seriously to affect the truth of the above statement. During locomotion the centre of gravity moves to the front and rear of the normal at rest; for example, in jumping it is in front of it when the fore-legs are coming to the ground, behind it when the hind-legs are leaving the ground; it is in front of it during draught, behind it during backing.

Distribution of the Weight of the Body.—The fore-legs carry more weight than the hind, which is perhaps the reverse of what might be expected; but if a horse be carefully weighed, it is found that the fore-legs take more than one-half the body weight. The position of the head (which may weigh as much as 40 and 50 lbs.) considerably affects the weight on the legs. Thus, if the head be raised up when the fore-legs are weighed, the latter will be found to be carrying over 20 lbs. less weight than if the head were dependent. The practical application of this fact is obvious —keep a stumbler well in hand. When a man is on the horse's back, it is found that 66 per cent. of his weight is carried on the fore-legs, and 34 per cent. on the hind; the amount of weight on the fore-legs is increased by leaning forward in the saddle, and decreased by leaning back. An explanation why fore-legs are worn out earlier than hind is afforded us by what we now know of the physiology of locomotion—viz., the fore-legs act as propellers of the body, and owing to their being nearest to the centre of gravity, they also bear the largest share of the weight of the body and the weight of the rider.

The Structure and Function of the Limbs in Relation to the Production of Lameness.—As high up as the shank we may say that there is no practical difference in the anatomical arrangements of the fore and hind limbs, and yet we know how commonly the foot and coronet of the fore-leg are affected with lameness, and how rarely in comparison the hind one. In comparing the knee and hock great differences are observed; it is true that in both a number of pieces of bone enter into their formation, but here the likeness ends; the small bones of the knee have considerable movement, the small bones of the hock only a trifling amount. The lower row of knee bones, so far as movement is concerned, are the nearest approach to the movement of the small bones of the hock, yet the latter are frequently diseased, the former rarely affected. Evidently, then, the presence of small and comparatively immobile bones in the hock cannot constitute an explanation of the frequency of hock disease. Does the manner in which the joints are flexed throw any light on the acknowledged fact that knee disease is rare and hock disease frequent? It will be observed that these two joints bend in opposite directions; the knee opens in the front when flexed, the hock opens at the back; we have already given reasons for believing that some injury may be inflicted on the hock-joint by its method of closing.

Continuing this comparison of the fore and hind leg, it may be remarked that the stifle corresponds to the elbow, and the patella to the ulna; during flexion of these joints the elbow opens at the back whilst the stifle opens in front: in other words, though corresponding joints—the elbow and the stifle, the hock and the knee—they do not agree in the direction in which their movement is made. The hip-joint corresponds to the shoulder-joint, and though in the hip all the movement is done by one bone instead of two, yet the to-and-fro movement is practically the same in each.

When the foré-leg comes to the ground, no matter what the pace may be, the limb must be straight in order that the foot may be placed down flat, or, as in the faster paces, heel first. This straightening of the knee renders the bony column of the leg rigid for the time being; the shock of impact is therefore greatest at that part of the column nearest to the point of impact, and decreases as it passes up the leg. It would be anticipating our subject to attempt to deal with the various means which exist in the foot to render this shock as little destructive as possible; we can only allude to the weight being supported on the laminæ, to the presence of a foot articulation which is yielding posteriorly, the existence of an elastic movement of the posterior part of the foot, and the presence of an elastic and indiarubber-like cushion, the foot-pad.

There are, however, two distinct strains imposed on a limb—viz., the shock or concussion when the foot comes to the ground, and the strain or compression occasioned when it is leaving the ground; one is the concussion of impact, the other the compression of propulsion. The hind-leg differs from the fore-limb in its method of providing for the concussion of impact; here we find that the limb instead of being straight—as the fore-leg is from the elbow to the foot—is bent, and it is bent at the hock, at a point which we may take to be midway between the stifle and the ground. The shock of impact comes, therefore, largely on the hock.

The fore-leg in providing for propulsion rotates over the foot, the limb still being straight from the elbow to the ground, and the shock of rotation is mainly confined to the lower end of the bony column. In the hind-leg propulsion is obtained not only by the foot remaining fixed on the ground, but also at the same time by a straightening or unbending of the hock, which gradually opens until the tibia forms with the metatarsal bone the nearest straight line it is capable of making. In this way we may say that the hock performs twice as much work as the knee, and such a statement throws some possible light on the frequency with which this joint is affected with disease.

The **Anti-concussion Mechanisms** existing in the limb are, roughly speaking, of two kinds—viz., (1) those for receiving the weight of the body on the leg when the foot comes to the ground, without the part suffering from the concussion of impact, and (2) those which admit of propulsion by one fore-limb without the parts suffering from the compression of propulsion. The first is principally provided by the yielding joints formed in the pedal and fetlock articulations, by the arrangement of the foot, and by the tendinous and ligamentous material at the back of the limb; the second is furnished by the column of bones forming the limb being broken up from the scapula to the pedis, and progressively increasing in size from the seat of the largest amount of compression—viz., the foot—to the least amount in the shoulder. Probably the coronet and pastern represent the weakest part of the fore-limb, and their small size in comparison with the weight they have to support is evidence of this.

To ease the skeleton from concussion the muscles and tendons are brought into play and rendered taut; we know, for instance, how much better a limb is prepared to stand a sudden shock if sufficient warning is given through the sense of sight.

The tendons and muscles of the limbs help to take the shock. So long as the muscles maintain their elasticity the work done by their tendinous attachments is comparatively slight; as the muscles tire the strain on the tendons increases, and in consequence they may give way, and this will occur at their weakest part. In this tired condition of limb the skeleton also suffers, the bones forming the column receive more shock than normal, and the smallest and shortest bones situated nearest to the seat of concussion, viz., the ground, may even fracture under the strain, and under any circumstances run a grave risk of becoming inflamed. This argument is based on clinical observation; we do not believe that any riding horse sprains its back tendons or suspensory ligament until the muscles tire, and are no longer capable of exhibiting that perfect elasticity inherent in muscular tissue. We do not, however, say that no horse suffers in its pastern bones until the muscles tire (for example the cart horse), though the strain on them is undoubtedly greater at this time than any other. The strain on the pastern bones during draught depends upon the force exerted, viz., the compression of propulsion, and that this is something considerable may readily be seen in any heavy draught work.

Fractures of the pastern also teach us some useful lessons; we may regard them for our purpose as experimental evidence of the shock inflicted on the lower bones of the limb. This shock is caused when the foot comes to the ground, not when it leaves it, and it may occur on hard ground or on sand; in the former case the cause of the concussion is obvious, in the latter at first sight it is not so clear, yet when we remember how rapidly horses tire when working at any fast pace over sand, and, owing to the nature of the ground, the manner in which they must misjudge the application of that muscular bracing which saves the skeleton from concussion, it is not difficult to explain the well-known fact that pasterns frequently fracture on sandy soil. Direct concussion in a horse which is not tired and is not working on sand may also produce a fracture of this region. Fractures of the pastern may occur from galloping horses on the wet sand of a seashore; this is the result of concussion: the next hardest thing to a macadamized road is a wet seashore.

Our only object in dealing with a subject which appears to be foreign to the one under consideration is to bring some light to bear on the strain to which the skeleton is exposed. This strain would appear to be greatest on the suffraginis in the fore-limb, for fracture of this bone is incomparably more common than fracture of the corona, though this might be accounted for by the density of the latter and the absence of a medullary canal. In concluding these remarks on fracture of the pastern, we would draw attention to the fact that the strain imposed on the bones in all cases is probably nearly identical in direction, for there is a remarkable similarity in appearance presented by fractures of either the corona or suffraginis, the fractured portions agreeing in shape and size, in some cases almost piece for piece.

In spite of what we have said about direct concussion affecting the pastern bones, we do not think that this is necessarily the only factor present in the production of ringbone. The compression of propulsion must take a part; we mean by this, the shock imparted to the pastern bones while the foot is on the ground and the body is passing over it. The fore-leg from the knee to the foot is only intended to open and close in one direction; we can readily make the foot touch the point of the elbow, but we cannot make it touch the front of the fetlock. Now if we study the movement the limb makes from the time the foot comes in contact with the ground, we observe that the fetlock at first descends and then ascends, and having reached the desired point the limb passes over the foot which remains fixed on the ground, and at this moment an important movement occurs in the pastern, viz., its rotation from rear to front. While the fetlock is ascending the metacarpal is moving on the suffraginis, the suffraginis on the corona, and the latter on the pedis; but as soon as the limb becomes vertical (in the rotation of the body over the foot), the movement between the suffraginis and corona becomes exceedingly limited, and for all practical purposes, *owing to their immobility, the two may be regarded as one bone*; thus the remaining rotation of the body occurs between the corona and pedis. It is only possible to understand this by following it out on the dead limb, the leg being upright and the foot fixed.

The important point is this—during the rotation of the body over the foot considerable compression and strain must be experienced in the pastern; this strain is most severely felt at the articulation between the suffraginis and corona, owing to the fact that these are *locked together* during the main extension of the limb. Further, as the upward and forward propulsion to the body is given as the foot is leaving the ground, much of the shock resulting from it must be expended on the pastern bones.

Irregularities in the ground surface are a severe strain on the coronets, especially of a horse out of condition. The study of hoof prints will readily demonstrate the fact of uneven tread; the lateral deviation of the coronet and pedal joints is something very small, yet every uneven tread, be it caused by a rut or a pebble, throws a strain on these parts, and there can be no doubt that many cases of ringbone originate in strains of the lateral ligaments of these joints.

In the **Act of Standing** the body is supported on four props; two of them have only a muscular attachment to the trunk, the other pair are united by a ball and socket joint. It is unnecessary to allude by name to the muscles connecting the fore-leg with the trunk, excepting the serratus magnus through the medium of which the body is principally slung on the scapulæ. No matter what the position of standing may be, the horse never, in a state of health, keeps its fore-feet in any other position than together; one fore-limb advanced in front of the other is abnormal excepting when grazing. On the other hand, it is very rare to see a horse standing squarely on both hind-legs, he is invariably resting the limbs alternately. Some years ago we drew attention to this as being an explanation of the exemption of the hind-limbs from navicular disease; by this process of resting, the compression of the navicular bone (through the body weight above, and the perforans tendon below) is relieved. The horse only learns to rest the fore-feet when too late.

In **Lying Down** the animal brings the four legs together under the body, and bends both knees and hocks, the knees and chest touching the ground before the hind-quarters. When down he either lies extended on one side or seated on the chest, two lateral legs being under the body and two outside it. If resting on the chest he inclines to one side or the other; he cannot like a ruminant lie plumb on the keel of the sternum owing to its sharp ridge. If inclined to the near side, the near fore-foot is placed close to the breast-bone, the elbow touching the ground, the near hind-foot is under the abdomen and he lies on the outside of the hock and shank; the off fore-foot lies close to the off elbow but as a rule outside it, and the point of the off hock touches the ground. A horse does not lie long in one position owing probably to the enormous weight of his body. It will be observed that the animal lies on the point of the elbow which is underneath the body. This is the cause of 'capped elbow,' and not that usually assigned, viz., resting on the heel of the shoe. When down the animal is either sitting on its chest or lying on its side, but in any case no position is maintained for any great length of time. He may sleep sitting on his chest, in which case he rests the chin on the ground with the lower lip frequently everted and so rests on the incisor teeth. The eyes are never completely closed, and he is the lightest sleeper imaginable.

Cattle repose on the breast with the head turned round to the side.

In **Rising** the horse can only get up by extending both fore-feet in front of the body; the hind-quarters are now pressed upwards, the animal securely fixing his toes in the ground, and assisted by the muscles of the back, the animal is immediately on his feet, the fore-part always rising before the hind. The ruminant rises quite differently, in fact the reverse of the horse, the hind-quarters being the first to ascend.

Locomotion. — We have now to study the question of locomotion in the horse, and describe how the legs are moved during the different paces. It will be remembered that our knowledge of this subject chiefly depends upon graphic records and instantaneous photography, the pioneers in the field being Marey* in France, Stanford, Stillman, and Muybridge in America.† We have selected typical studies in order to elucidate the text, but it must be remembered that no hard-and-fast attitudes can be adopted. The sharp quick clever horse whose muscular response is rapid does not move his legs quite in the same way as the slow lethargic indifferent type; and similarly a tired horse moves differently from one whose muscles are fresh and responsive.

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* 'Animal Mechanics,' International Scientific Series.

† 'The Horse in Motion.'

The **Walk** (Fig. 126) is the slowest pace, the movements are somewhat complex, and may roughly be divided into four stages. In the first the body is balanced on three legs, in the second stage on two diagonal legs, in the third on three legs, in the fourth on two lateral legs, and the next movement brings it back to the first stage, only with different legs employed. Tracing the movements in each stage, the horse advances one fore-leg—say, the off (Fig. 126, *1*)—and is left standing on the near fore, near hind, and off hind; in the second stage the near hind is

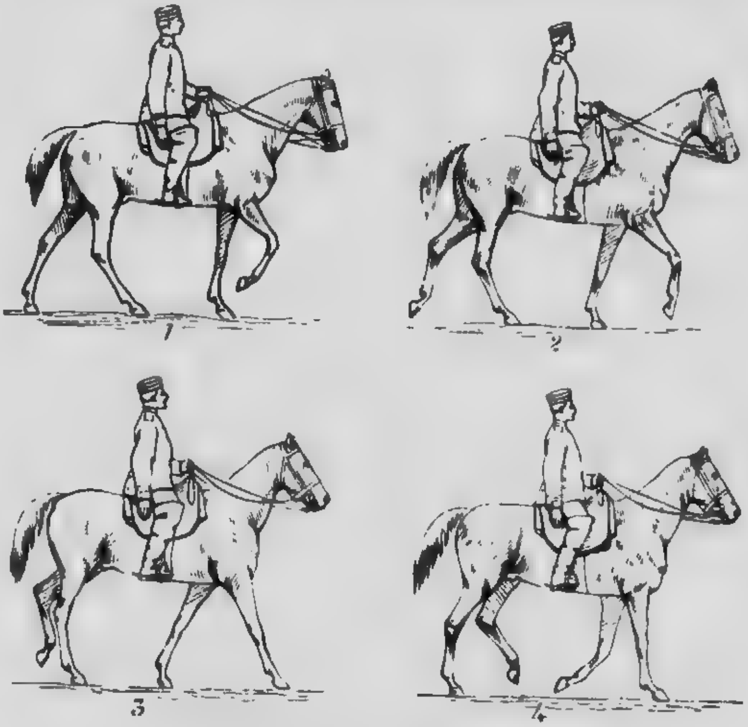

FIG. 126.—THE WALK (ELLENBERGER).

picked up, and the animal is standing on the near fore and off hind, viz., on diagonal legs (Fig. 126, *2*); in the third stage the off fore has come to the ground, and the animal is balanced on both fore and the off hind leg (Fig. 126, *3*); in the fourth stage the near hind is advanced to be placed over, or in advance of, the track of the near fore; to make room for it the near fore is advanced, and the horse is left standing on two lateral legs, viz., off fore and off hind (Fig. 126, *4*). The next movement brings the animal into the first position, with the near fore leading instead of the off fore. The fore-leg remains on the ground for a longer time than it takes in passing through the air, and comprises the period during which the body is passing over the limbs. The movement in the air both of fore and hind legs is so extremely rapid as almost to defy detection. The snatching up of the foot from the ground is the quickest movement. Stillman refers it to the spring or rebound of the suspensory ligament, but it is doubtless due entirely to the flexor muscles. In walking on level ground the majority of horses rarely extend the knee any great distance beyond a vertical line dropped from the point of the shoulder. A sudden movement of the extensors now straightens the leg, and the foot is placed down flat or heel first. If the leg is not fully straightened by the extensor muscles, the foot comes to the ground toe first, with the knee slightly bent, and a stumble follows. In heavy draught work it is no uncommon thing to see the toe put down first, but here the conditions are very different. It appears to be a matter of indifference with which fore-leg an animal starts the walk; under some conditions he may indeed make the first step with a hind leg, in which case the next to move is the corresponding fore-leg in order to make way for the hind foot.

The **Trot** (Fig. 127) is a very simple pace to analyse; the body is supported on diagonal legs (Fig. 127, *1*), which by their propulsion drive it off the ground, during which period all the legs are in the air (Fig. 127, *2*); when the

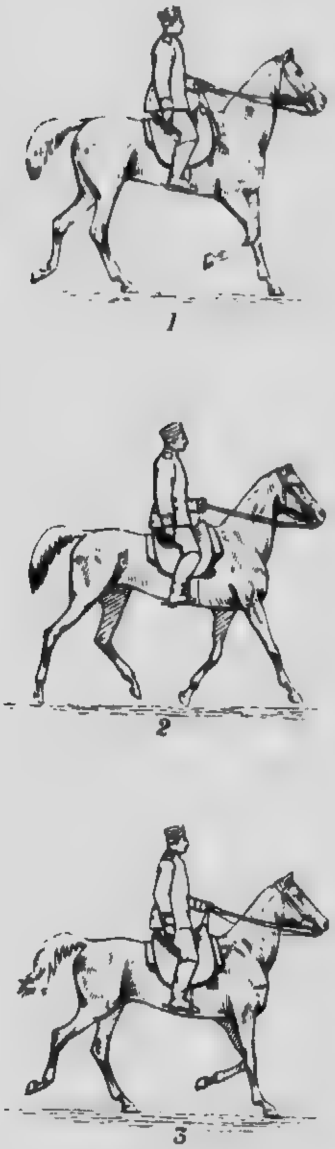

FIG. 127.—THE TROT.

From instantaneous photographs by O. Anschütz. (Ellenberger.)

body comes to the ground again the next pair of diagonal legs receive it (Fig. 127, *3*), and once more propel it. There are thus three stages to the trot; the body in two of them is supported by diagonal legs, and in one of them it is in the air.

The trot appears to be the only pace in which instantaneous photography has supported the conventional notions of this movement. We can see the trot, first because it is a simple pace, and secondly because the body is comparatively long in the air. When a horse falls at the trot, he does so either through not flexing his knee sufficiently before bringing the leg forward, or the extension of the knee is not perfect, and in consequence the limb is unfit to stand weight. The knee should be sufficiently but not unduly bent and the leg brought rapidly forward, the limb then sharply extended, well braced, and the foot placed firmly on the ground heels first.

In the **Amble** the horse, instead of using diagonal legs uses the lateral limbs, so that off fore and off hind are on the ground instead of off fore and near hind. An animal may amble both at the walk and trot, in this respect resembling a camel. There is no doubt that it is a perfectly natural pace for some horses; others are taught it, as it is a particularly pleasant one for the rider and less fatiguing for the horse.

In the **Canter** (Fig. 128) the body is pushed upward off the ground by one fore-leg—we will say the off fore (Fig. 128, *1*)—the near fore and both hind being off the ground; in the next stage all the legs are off the ground though the feet are no great distance from it (Fig. 128, *2*); in the third stage the body returns to the ground, alighting on the near hind-leg, which is not placed under the centre of gravity as in the gallop, but behind it, the animal being balanced on one limb only (Fig. 128, *3*); in the fourth stage the off hind and near fore come to the ground together, so that the body is now balanced on three legs—viz., near fore and both hind (Fig. 128, *4*); in the fifth stage the off fore comes to the ground, but as it does so

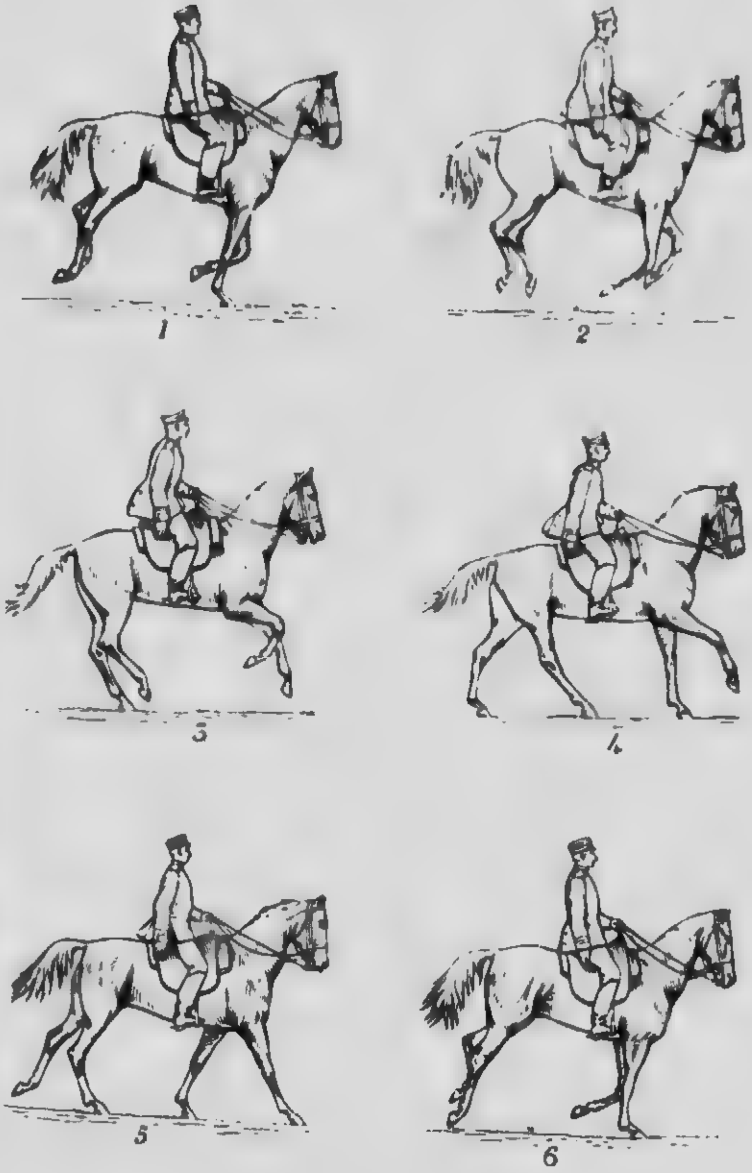

FIG. 128.—THE CANTER.

From instantaneous photographs by O. Anschütz. (Ellenberger.)

the near hind rises; the animal is still left on three legs—viz., both fore and off hind (Fig. 128, *5*); in the sixth stage the near fore and off hind leave the ground, the horse being balanced on the off fore only (Fig. 128, *6*); the next movement is a repetition of the first, the off fore pressing the body upwards. In the example quoted the off fore is the leading leg, and it will be seen that it is this which gives the final propulsion to the body. This is the explanation of why the leading leg tires so early. Though it is a matter of indifference which leg a horse leads off with in the walk and trot, this is not the case in the canter or gallop. There are some animals which, so long as they are leading with the leg of their own choice, are pleasant in their paces, but if forced through fatigue or other cause to lead with the opposite fore leg, their movements are rough and clumsy and wanting in co-ordination. It should form part of the training of every horse to teach him to change his leading leg in the canter or gallop with facility; this education would prevent many cases of sprain.

The **Gallop** is a very difficult pace to describe, and the analysis I give of it here is from one of Muybridge's numerous instantaneous photographs.

The gallop (Fig. 129) consists of seven stages; for simplicity we will elect to describe it from the time the animal is in the air, with no legs on the ground, but all four of them brought well under the body; this is the first stage (Fig. 129, *1*); in the second stage one hind-leg, say the off, comes to the ground, the foot being placed down close under the centre of gravity and not behind it as in the canter (Fig. 129, *2*); in the third the near hind comes to the ground, the horse now being balanced on two hind-legs, both fore being in the air (Fig. 129, *3*); in the fourth stage the off fore comes to the ground, but the animal is not balanced on three legs as in the canter, for at the moment the off fore comes to the ground the off hind is extended, leaving the horse on diagonal legs—viz., off fore and near hind (Fig. 129, *4*); in the fifth stage the near hind leaves the ground, the animal being balanced on the

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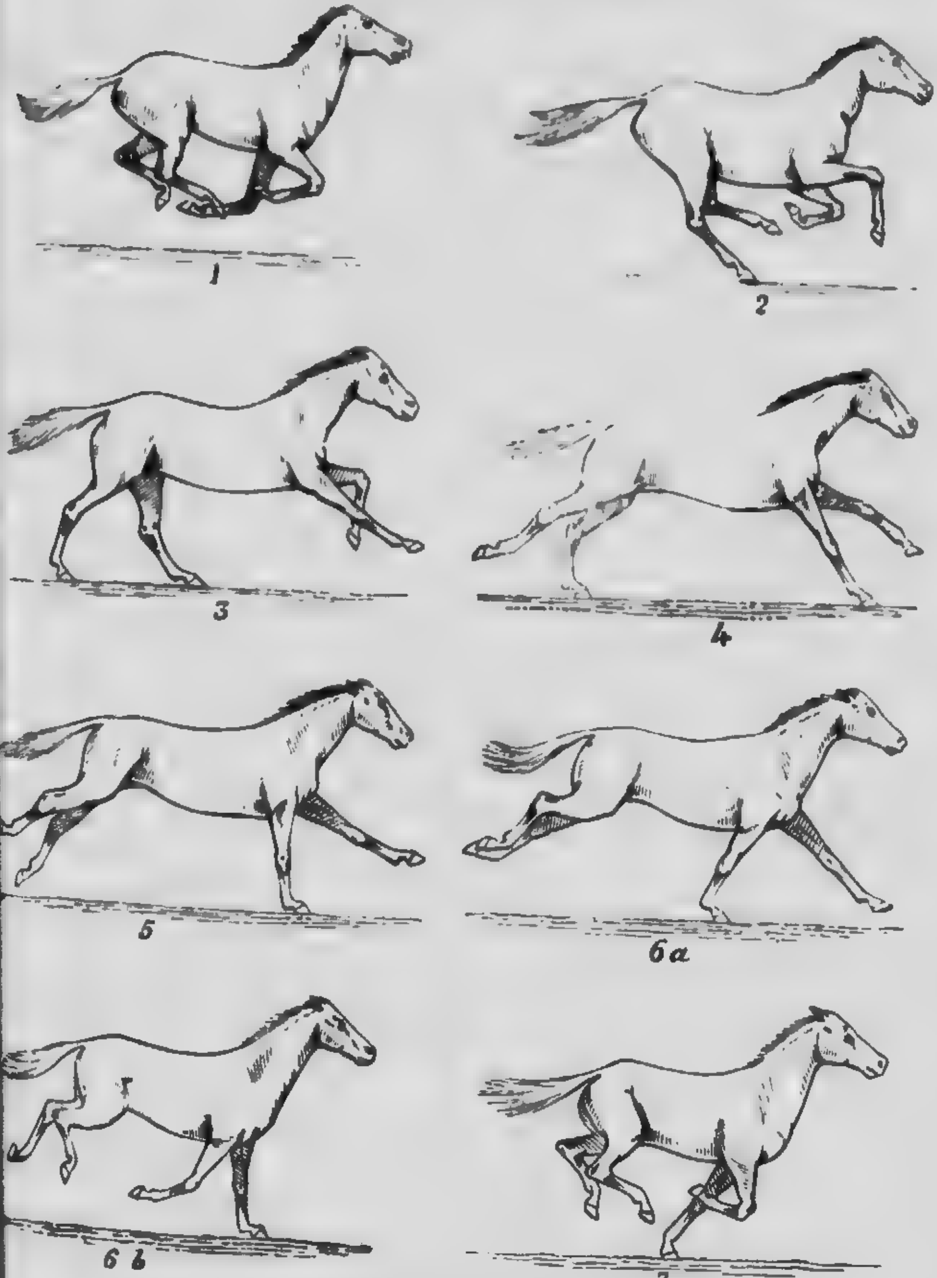

FIG. 129.—THE GALLOP.

After Stanford, Muybridge, and Stillman. ('The Horse in Motion.')

off fore-leg (Fig. 129, *5*); in the sixth stage the near fore comes to the ground (Fig. 129, *6a*), and the off fore leaves it (Fig. 129, *6b*)—the body is still supported on one fore-leg; in the seventh stage the body passes over the near fore-leg (Fig. 129, *7*), and by a contraction of its muscles the entire weight is lifted off the ground, and propelled forwards and upwards (Fig. 129, *1*). The simplest description of the gallop is that the horse takes a stride with the hind-legs which then leave the ground; he next strides with the fore-legs, and at the end of this propels the body for several yards through the contraction of the muscles of the fore-leg on which he was last bearing. During the true gallop he never has more than two legs on the ground at the same time, and they are always pairs, excepting in position *4*, Fig. 129.

The points of importance in both the gallop and canter are that the heel of the foot comes to the ground first, that the hind-legs break the shock of the falling body, and that the fore-legs take the largest share in propelling the weight. Two of these facts were described years ago by Lupton, but were not accepted.* In examining the track of a galloping horse it is remarkable to observe what a very straight line the hoof-marks leave, showing that each foot is brought well under the middle line of the body. When a horse gallops, no matter how fast the pace, the fore-feet never extend beyond a vertical dropped from the muzzle.

In the **Jump** (Fig. 130) the horse rises to it by the propulsion upwards which the fore-legs give to the body (Fig. 130, *1*), the knees at the same time being flexed to enable the feet to clear the obstacle. Both hind-legs being fixed on the ground, the body is through these propelled forwards (Fig. 130, *2*). In alighting the animal does so through the medium of the fore-legs, either together or one following the other but always straight (Fig. 130, *3*). Instantaneous photography disproves the theory that in the jump a horse naturally alights on the hind-legs, though it is true that some clumsy horses do.

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* See footnote, p. 559.

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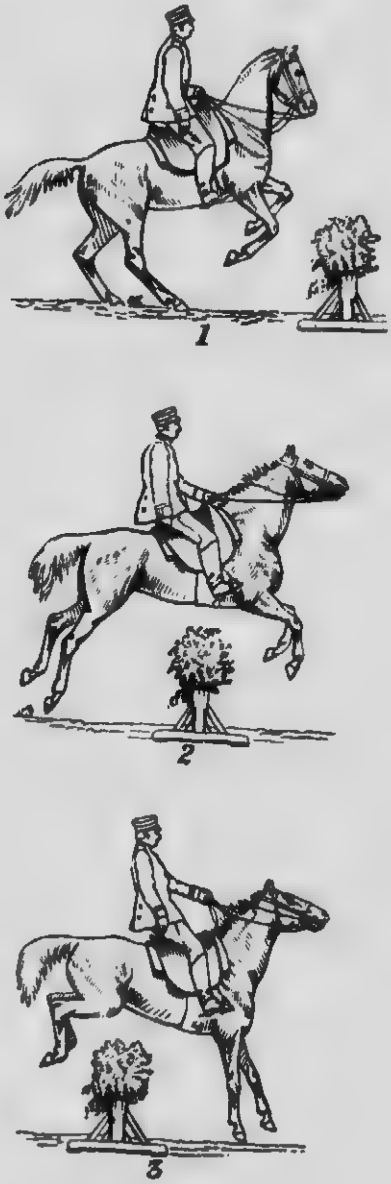

FIG. 180.—THE JUMP.
(*Anschütz-Ellenberger.*)

In **Rearing** the hind-legs are brought well under the body, the head and neck are thrown up, and the propelling power of the fore-legs directs the body upwards, where it is sustained by the muscles of the back and loins. So long as the centre of gravity falls within the base formed by the hind-feet, the body is in a position of stable equilibrium; but if it passes outside this, the horse comes back on to the point of both hocks, and may either roll over on its side or go directly backwards. If the latter, the first part of the body to strike the ground is the occiput; in this way fracture of the base of the skull may occur.

In **Kicking** with both hind-legs the head is depressed, and a powerful contraction of the muscles of the quarter and back throws the croup upwards, and at the same time both legs are violently extended. Kicking may be practised either with one hind-leg backwards or one hind-leg forwards. The latter is very dangerous; fortunately only an accomplished horse can effect it; it is known as 'cow-kicking.' Owing to the pubo-femoral ligament a horse can only kick outwards with difficulty. Striking with the fore-feet is not common, and is not characteristic of British horses, nor are 'cow-kicking' or 'buck-jumping.'

In **Buck-jumping** the animal springs bodily off the ground, the head being suddenly depressed between the fore-legs and the back violently arched.

The Normal Daily Work of Horses, the rate at which they are capable of performing it, and the power they exercise in doing so, must now be briefly considered. Rankine has laid down that **mechanical daily work** is the product of three quantities: (1) the effort; (2) the rate; (3) the number of units of time per day during which the work is continued. Our only difficulty is in obtaining the value of the effort, which it is clear must depend upon the nature of the work, the character of the ground, the weight carried or drawn, and the physical fitness of the animal. The normal work of horses would appear to be 3,000 foot-tons per diem; a hard day's work is equivalent to 4,000 foot-tons, and a severe day's work is 5,000 foot-tons. Redtenbacher* places the daily work of a horse for 8 hours at 6,700 foot-tons, and Rankine's tables † show that a draught horse exercising a force of traction of 120 lbs. for 8 hours a day, performs 6,200 foot-tons of work. I think both these estimates are without doubt too high. The co-efficients of resistance employed in our calculations were those determined for man by the Rev. Professor Haughton; we know of none specially calculated for the quadruped. Assuming the weight of the animal, plus the weight carried or drawn, to be equal to 1,000 lbs., then 3,000 foot-tons of work will be obtained by the following work:

Walking	at	3	miles per hour	for	8·7	hours.
,,	,,	4	,,	,,	5·8	,,
,,	,,	5	,,	,,	3·7	,,
Trotting	,,	8	,,	,,	1·5	,,
Cantering	,,	11	,,	,,	1	,,

This table is only given as a means of conveying to the mind the value of 3,000 foot-tons of work, though trotting 12 miles or walking 18½ miles are commonly done in practice as a day's work.

The **Velocity** of the gallop has been variously stated, but it is certain that no horse has galloped 1 mile in 1 minute as is reported of Flying Childers. A horse named Salvator in 1890, carrying 7 stones 12 lbs., was galloped on a straight course against time, and did a mile in 1 minute 35½ seconds. The most severe galloping ever recorded was performed by Quibbler in 1786, who galloped 23 miles round the flat at Newmarket in 57 minutes 10 seconds. The fastest pace at which trotting has been performed is 1 mile in 2 minutes 8¼ seconds. The celebrated American trotting-horse Tom Thumb trotted 100 miles in 10 hours 7 minutes, including a stoppage of 37 minutes; an English mare did the same distance in 10 hours 14 minutes, including a stoppage of 13 minutes, while Sir E. Astley's Phenomenon trotted

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* Quoted by M'Kendrick.

† 'Encyclopædia Britannica,' art. 'Animal Mechanics.'

17 miles in 53 minutes. All the old performances here quoted are from Youatt's work on 'The Horse.'

Turning now to what may be expected of ordinary horses, it may be noted that the average walk of a cavalry horse is 3·75 miles per hour; the average trot is 7·5 miles per hour, or a mile in 8 minutes, and a fast trot is 8½ miles per hour. A gallop is from 12 to 14 miles per hour. The stride of horses at various paces was measured in a very ingenious manner by Stillman and Muybridge. They give the stride at the walk as 5 feet 6 inches; at the trot between 7 feet and 8 feet; at the canter about 10 to 12 feet; and the gallop between 16 feet and 20 feet—they even speak of a stride of 25 feet. An American pacer has been known to cover 21 feet in a stride.

The question of the **Weight** which a horse can carry is one affecting the vital interests of the cavalry service; there is a great difference between the actual or total weight a horse can carry and the *effective* weight he can carry.

The question of weight is greatly influenced by the pace at which it has to be carried, and under any circumstances is largely governed by the weight of the animal's own body. We have shown that horses should not be asked to carry more than one-fifth of their body-weight, and this conclusion will doubtless apply to all riding horses.* One-fifth of the body-weight of a cavalry horse is roughly 14½ stones; instead of this they carry about 20 stones.

The physiological features of **Draught** can only be glanced at. The subject of draught is a complex one, and our information is still very incomplete. Quadrupeds appear to be designed for the purpose of draught, a horizontal spine is not intended for carrying weight; such can only be satisfactorily met by an upright column, as in man, who from his conformation is essentially devised for carrying a burden; the horse, on the other hand, is constructed for hauling or draught. Brunel, in his article on 'Draught,'† points out that the reason why a horse is more suited for draught than for carrying weight, is that he can throw his weight considerably in front of his centre of gravity, the feet forming the fulcrum, and 'allowing the weight of the body in its tendency to descend to act against the resistance applied horizontally and drag it forward; as the resistance yields the feet are carried forward and the action continued.' Such is the theory of draught. The nature of the vehicle, the condition of the roads, the angle the trace forms with the horizontal, the presence or absence of springs, four wheels or two, high or low front wheels, and the width of the track, are features which singly or combined greatly complicate the question.

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* 'The Effective Weight Horses can Carry,' *Journal of Comparative Pathology and Therapeutics*, vol. xi., No. 4.

† 'Book of the Horse,' Youatt.

The force exerted in draught depends upon the load and the pace; in the light or mail stage-coach, where 10 and 11 miles an hour were attained, the strain or force of traction employed by each horse was only 40 lbs.; in the heavy coach it was 62½ lbs. for each horse. The higher the velocity the less the force of traction which can be employed, and the shorter the duration of labour. For slow draught work at 2½ to 3 miles per hour, and for 8 hours a day (which appears to be the most suitable pace and duration of labour), a force of traction of from 100 lbs. to 125 lbs., or 150 lbs., is quoted by Brunel as being the most suitable. But a force of traction of 120 lbs. for 8 hours a day is too much to expect. Watt found that a horse could raise a weight of 150 lbs. passed over a pulley, 220 feet per minute. This, as applied to engines, is termed 'horse power,' and is equal to 33,000 lbs. lifted 1 foot high per minute, 33,000 foot-pounds per minute. This standard of comparison cannot be generally applied to horse labour, as it is far too high. An animal could only perform this amount for 3½ hours per diem, whereas its most useful work is performed in 8 hours.

The actual dead pull which a horse can exert depends upon his body-weight; no animal tested by me against a dynamometer has pulled his own weight, nor should we expect it. From 65 to 78 per cent. of the body-weight was found by us to represent the maximum muscular effort of the horse.[*] The animals tested were grouped according to the spirit they put into their work:

Group 'excellent' pulled 78·5 per cent. of their body-weight.
„ 'good' „ 77·6 „ „ „
„ 'fair' „ 70·6 „ „ „
„ 'bad' „ 65·6 „ „ „

Pathological.

The question of lameness in horses must always occupy a prominent position in veterinary practice. It is intimately bound up with the locomotor apparatus, and it is not possible to attempt any useful summary of the troubles met with. The anatomy and physiology of the locomotor system should be thoroughly understood by the student if he is to become a good practitioner.

[*] 'The Maximum Muscular Effort of the Horse,' *Journal of Physiology*, vol. xix., 1896.

CHAPTER XVII

THE FOOT

THE foot is largely a modified form of skin, the vascular tissues represent the corium, while the horn represents the epidermis. It is no uncommon thing to have a horn-like tissue produced by the skin, as, for example, in the human nail, in the hand of the labourer, and in the chestnut and ergot found on the limbs of the horse. In spite of its origin from the skin, the foot is a specialised structure presenting not only a surface for wear and tear, but mechanisms for supporting the weight, and others devoted to warding off from both the foot and limb the concussion and jar to which such a structure is necessarily exposed. If it were not for the mechanisms just alluded to, and were the foot a structure simply devoted to offering a surface of sufficient density for the horse to stand upon, it would present little of special interest.

The foot may primarily be divided into two parts, the insensitive or horn foot and the sensitive or vascular foot. The horn is produced from the vascular foot, but the latter does not exist solely for the production of horn; it is provided with a fibrous pad, elastic tissues, a peculiar arrangement of joint, and a remarkable corium, the collective function of which is devoted to saving the parts from destruction during the battering process to which the foot is exposed, and further to support the weight. These two feet the sensitive and insensitive are closely united; in their general configuration one is an exact counterpart of the other, and one fits into the other much as a finger fits into a glove. It would be out of place here to give anything like a detailed account of the anatomy of the foot, but there are certain structural features so intimately associated with the physiology of the organ that it is impossible to separate them.

Bones of the Foot.—The core of the foot consists of bone around which all the other structures are moulded. The bone is not one solid piece, as we might imagine would be necessary in such a position, but on the other hand consists of three pieces. One of these is the pedal bone which in shape resembles a miniature foot, and the substance of which is porous to such an extent as to resemble pumice-stone in appearance. A second bone, the navicular, is very small, of peculiar shape, dense in structure, rests slightly on the pedal bone, and is mainly held in position by ligamentous tissue. The third bone only belongs partly to the foot and partly to the limb. One would suppose that the pedal bone should occupy the whole of the interior of the hoof, as high as the coronary edge and as far back as the heels, but this is not so. It only occupies a comparatively small portion of the internal foot (Fig. 131), and that portion is mainly situated towards the anterior and lateral parts; the posterior part of the foot contains very little pedal bone, but the deficiency is made up by the introduction of two large plates of cartilage attached to the bone, and over which the structures are reflected and moulded as on the bone itself. This singular deficiency of bone, in a part where one might be led to regard its existence in large amounts as a necessity, and the presence of large cartilaginous plates to take its place, is due to the various movements which the foot has to perform, and which could not be carried out if the bone of the foot were relatively proportioned to the structure within which it fits.

The Foot-joint.—Three bones form the foot-joint. The question naturally arises why the joint is not composed of two bones instead of three, and what advantage is gained by the introduction of a small dense bone such as the navicular into the articulation? The articulation furnished by the pedis is much smaller than that furnished by the corona, but by the introduction of the navicular, the pedis plus navicular surface is nearly but not quite equal to the corona surface; one use, therefore, of the navicular bone is to increase the articular surface of the pedis. But it is conceivable that this small articular surface of the pedis might have been increased in some other way than by the introduction of a distinct bone and other complicated apparatus, and one is forced to recognise that the value of the navicular articulation does not depend entirely on the fact that it increases the size of the joint, but that it supplies what elsewhere we have spoken of as a yielding articulation. The value of this yielding articulation appears to be in the saving of direct concussion; the weight through the corona comes in the first instance mainly on the navicular, which under its influence yields slightly in a downward direction; from the navicular the weight is transferred to the pedis itself, which, as we shall later have to point out more particularly, also yields slightly under its influence, and in this way it is undoubted that direct concussion to the joint is prevented.

The Navicular Bone and Bursa.—It is quite certain that the navicular would be of very little use for the above purpose, if it depended on being kept in position solely by the delicate ligaments which have origin from it. The chief support to the navicular bone is the broad expansion of the perforans tendon which passes beneath it; between the tendon and the bone the most intimate fitting occurs, and a synovial apparatus exists here to save friction. It is probable that the perforans tendon and the inferior face of the navicular are more closely adapted to each other than any articulations in the body, excepting those found in the knee and hock joints. Briefly, then, the small dense navicular bone is enabled to form a yielding articulation in the foot, owing to the manner in which it is supported in position by the powerful perforans tendon. It might be argued on purely theoretical grounds that a small bone thus placed in the foot would be very liable to damage, and such we know practically to be the case.

It is not our intention here to touch on the subject of navicular disease, excepting in so far as it helps to elucidate the physiology of the part, but it is permissible to regard the lesions of navicular disease in the light of a physiological experiment, and we learn from them how intimately the freedom and elasticity of a horse's action depend upon the navicular bone, and the stilty, pottering, shuffling gait conferred on the animal when the navicular bone is no longer capable of properly performing its functions. The very close support afforded to this bone by the perforans tendon may possibly be a cause of disease, for the conclusion has been forced on us that under the influence of the weight of the animal, and the counteracting influence of the perforans tendon, the navicular bone must be exposed to considerable compression (see Fig. 131). This view is mentioned here not so much as a pathological as a physiological factor.

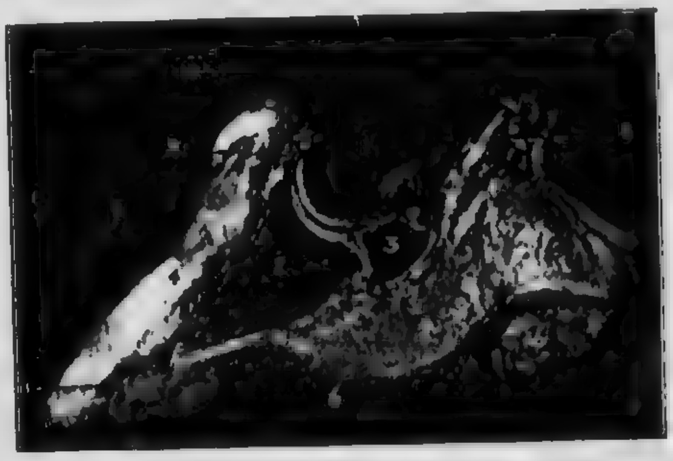
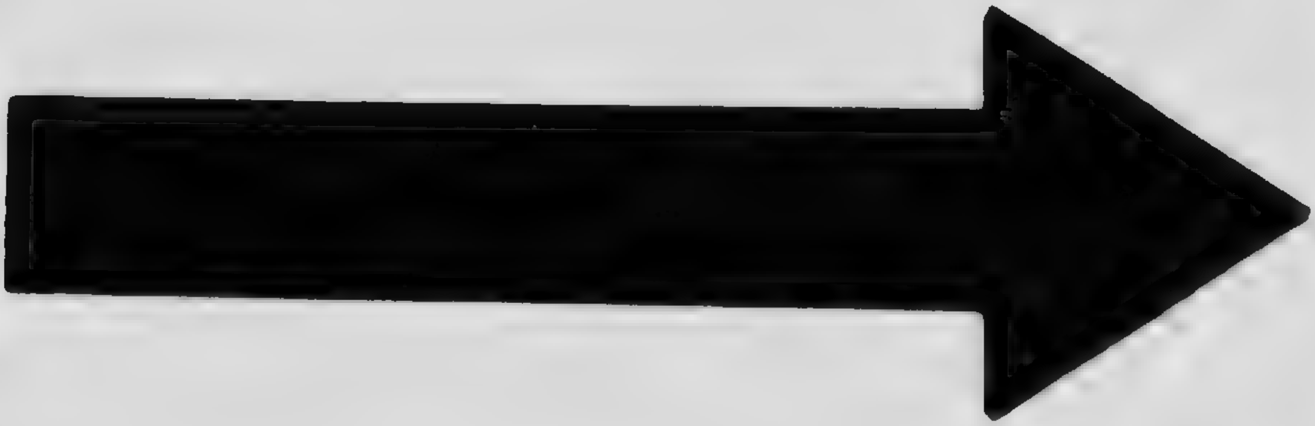


FIG. 131.—LONGITUDINAL SECTION OF THE FOOT.

1, The corona; 2, the pedis; 3, the navicular; 4, the horn wall; 5, the horn sole; 6, 6, the foot-pad; 7, 7, the plantar cushion; 8, the perforans tendon passing under the navicular bone, to be inserted in pedis; 9, the wall-secreting substance; 10, the extensor pedis tendon; 11, junction of wall and sole, the 'white line.'

We cannot recognise in the navicular bone any pulley function in connection with the perforans tendon, such as has been usually described, that is if by the use of the term pulley it is sought to convey the impression that some mechanical advantage is obtained. It is true that by passing beneath the navicular bone the direction of the pull of the tendon is slightly altered, but no mechanical advantage is thereby derived. The perforans tendon at its insertion spreads out fan-shaped, and is attached over a considerable semilunar surface of the pedal bone; so extensive is this attachment that it is erroneous to believe the tendon plays over the navicular bone. It is true that movement does occur between the tendon and the bone, but the tendon is passive, while the yielding of the navicular bone under the influence of the body-weight is the active agent. It is curious to observe the direction in which the largest amount of friction occurs between these two surfaces. Reasoning from the position of the parts one would think the greatest amount of wear must occur at the moment the foot comes to the ground, but if the eroded tendon of navicular disease be examined, it will be observed that the fibres are all stripped *upwards* and rarely or never downwards. This would point to the greatest friction occurring, not when the bone yields under the weight, but when it returns to its place as the body passes over the foot; but it may be that the fact is capable of a different explanation. The frequency with which the central ridge of the navicular bone is affected with disease, would point to this part as being the position of the largest amount of pressure.

Lateral Cartilages.—Attached to the heel of each pedal bone is a large curved plate of cartilage, in parts fibrous, in others hyaline in nature. So extensive is this plate that it reaches high above the margin of the hoof—viz., outside the foot in an upward direction as far forward as the coronet and as far back as the heel (Fig. 141, p. 568). There is no other structure in the body with which it can be compared: a bone possessed of two large cartilaginous wings is a something peculiar to the foot. The use of these cartilages is intimately connected with the main



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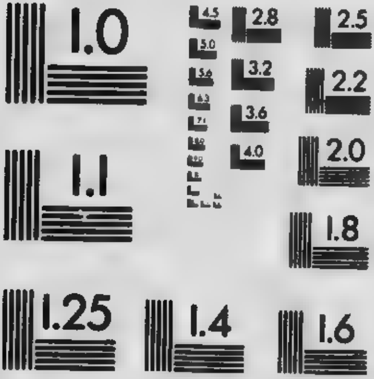

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principles of the physiology of the foot, to be dealt with later.

Plantar Cushion.—Placed between the two plates of cartilage is a large somewhat pyramidal-shaped body known as the plantar cushion (Fig. 131, *7, 7*). In appearance it resembles a fibro-fatty mass, composed of interlacing fibres and fat, pale yellow in colour, almost destitute of bloodvessels, firm to the touch, yet yielding in its nature. It occupies the posterior part of the foot, rising above the hoof into the hollow of the heel, whilst its inferior face is V-shaped, and a complete counterpart of the horn cushion or food-pad which covers it.

The **Corium** of the foot completely covers the structures just described, viz., the whole of the pedal bone, a large surface of the lateral cartilages, and the plantar cushion. This tissue has received various names—viz., from its colour the vascular foot, from its appearance the fleshy, from its character the velvety foot, whilst from one of its functions it has been termed the horn-secreting foot.

The **Vascular Wall** or **laminal tissue** (Fig. 132-2) is composed of a number of leaves lying side by side, which run from the coronet downwards and forwards to the edge of the wall. In number there are about 500 or 600, and they invest the entire surface of the pedal bone and the greater part of the lateral cartilages, their extreme vascularity giving the appearance of a thin layer of muscle. The leaves at the toe are longer than those at the heel, where they are short and turned in under the foot, running forwards beneath it to form the sensitive bars.

If a single leaf, say at the toe, be removed and examined, it is found to commence immediately under the thick cornice-like structure known as the coronary substance, and to be most firmly attached to the pedal bone; in fact, so intimate is the attachment that it is almost impossible to remove this tissue cleanly from the bone. The edge of the leaf is not regular but denticulated, and when viewed from its face it is observed that it is narrower near the coronet than at its inferior part, at which latter place it terminates in five or six papillæ. The leaf is extremely vascular, in fact quite scarlet in colour, the effect over the whole mass of leaves being very striking in appearance. If the tissue be examined microscopically it is found that part of its substance is devoted to leaf formation, whilst the remainder is a sub-laminal tissue, the function of which is to secure the laminæ firmly to the wall of the pedal bone. This sub-laminal tissue has been described by Moeller as consisting of two layers; the one nearest the bone is designated the *stratum periostale*, and acts as the periosteum of the bone (Fig. 133, *e*). Outside this is a layer of fibrous connective tissue and elastic fibres, arranged in bundles, crossing and forming networks, and containing few cellular elements, though more than were found in the periosteal stratum; this layer is extremely vascular and has been designated the *stratum vasculosum*. External to this layer are the laminæ formed of elastic and connective

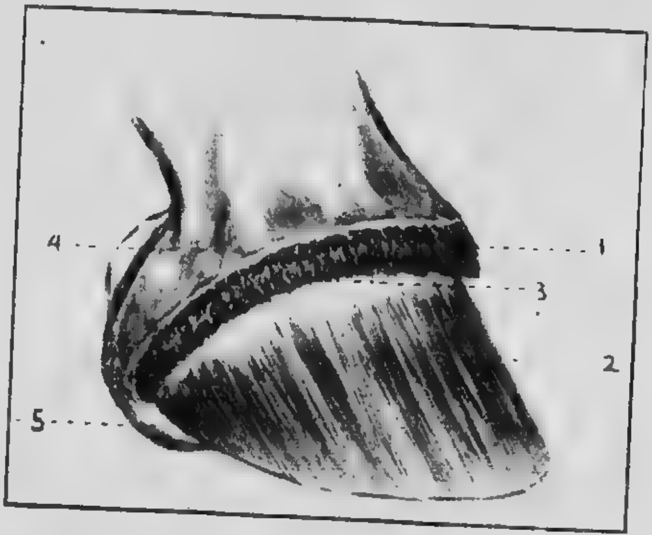

Fig. 132.—The Vascular Wall, the Hoof being removed.

1, The wall-secreting substance with its papillæ; 2, the sensitive laminæ; 3, where the upper end of the sensitive laminæ run into and fuse with the coronary substance; 4, a line between 1 and the skin, which secretes the periople; 5, the heels of the plantar cushion.

tissue fibres as in the previous layer, only the network is much finer. The laminæ contain numerous bloodvessels and nerves.

If a horizontal section of the laminæ be made and examined microscopically, it can easily be seen that each lamina has growing from its free edge a number of delicate processes which are miniature laminæ, or as they have been termed secondary laminæ or lamellæ (Fig. 133, *d*); in

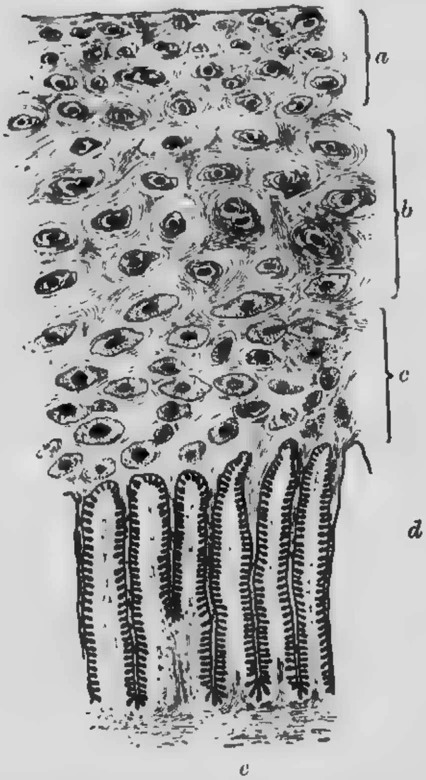

FIG. 133.—HORIZONTAL SECTION OF THE HORN AND VASCULAR WALL OF THE HORSE'S FOOT. LOW MAGNIFICATION.

a, *b*, *c*, The outer, middle and inner portions of the wall, showing the canal system with the tubular and intertubular horn; *d*, the horn laminæ bearing on their side the lamellæ, shown black; there are sometimes a few short laminæ to be seen, one is shown in the figure; *e*, the sub-laminal tissue, from which the sensitive laminæ may be seen dovetailed between the horn laminæ, and from the sides of which grow the sensitive lamellæ.

number they are from 100 to 120 on each leaf, depending upon the size of the primary lamina. The appearance thus presented (Fig. 133, *d*) is very characteristic, and has been likened by Chauveau to a feather, the barb being the lamina and the barbules the secondary laminæ.

The **Wall-secreting** or **Coronary Substance** is a thick, half-round, cornice-shaped welt of material situated above the laminæ (Fig. 132, *1*); it has received several names, the most rational being that based on its function as the wall-secreting substance. Externally this body is covered by a membrane possessing long papillæ which are highly vascular, and readily seen by immersing the foot in water, while the body itself on section is fibro-fatty in appearance. It extends all round the coronet from heel to heel, and here joins the plantar cushion. On its superior margin is a narrow groove (Fig. 132, *4*), which is the dividing line between skin and hoof, and from which the periople is secreted. On the lower margin the substance fuses with fibres from the sensitive laminæ. The entire coronary substance fits into a half-round groove in the wall, and the papillæ on its surface are lodged in canals formed in the horn. Beneath the coronary welt is a well-developed subcutis, which unites it to the tissues covering the corona and to the lateral cartilages. The vascular papillated membrane covering the coronary substance is irregularly pigmented, corresponding to the colour of the horn wall.

The **Vascular Sole** is scarlet in colour, and covered by long papillæ which are lodged in the horn sole. In each papilla an artery and one or more veins may be found.

The corium covering the plantar cushion is similarly arranged, the papillæ being lodged in the foot-pad or horn frog.

The **Blood Supply** the foot is exceedingly rich. We have alluded to scarlet appearance presented by the laminæ, the vascular sole, and the tissue covering the plantar cushion; but besides these the coronary cushion, pedal bone, etc., are richly supplied with blood. The pumicestone-like appearance presented by the latter is for the purpose of affording passage to the innumerable vessels which are passing from the interior of the bone in an outward direction to reach the vascular tissues; in fact, no description or drawing can adequately convey an idea of the appearance presented by this vascular body. The veins are large and numerous (Fig. 134) and are not provided with valves; some pass through the substance of the lateral cartilage, and a large plexus exists both outside and inside the cartilage. The relation of these vessels to the lateral cartilages and the absence of valves are points which will occupy our attention again when we deal with the use of the various parts of the foot.

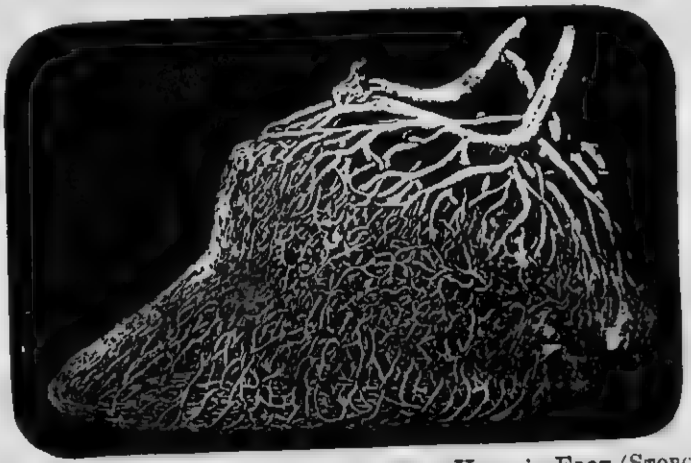

Fig. 134.—The Venous System of the Horse's Foot (Storch).

The insensitive foot or **Hoof** is moulded over the sensitive structures in such a way as to cover them completely, and form in horn a perfect counterpart of the sensitive foot. The hoof is composed of a wall with its inflections the bars, a sole, and a foot-pad or frog; each of these parts must be considered separately.

The **Wall** is that part of the hoof which can be seen when the foot is on the ground; its division into toe quarters and heels is for convenience of description, as no natural division exists. On the exterior of the wall is a layer of horn known as the periople, which is mor apparent near the coronet where it is white, soft, and thick

(Fig. 135), than lower down where it is extremely thin and more of the nature of a varnish, while at the toe it is practically absent. This layer is formed from the upper edge of the coronary substance. In a foot which has been poulticed, the periople at the coronet stands out as a white band running from heel to heel; this appearance is due to the absorption of water by the layer of soft cells of which it is composed at the coronet. The use of the periople appears to be to cement over the junction of the skin and hoof, and by the covering it affords the wall to assist in preventing evaporation from its surface. The colour of the wall is black, or black and so-called white, really buff; a black horn is produced by a pigmented coronary substance, a buff horn has no pigment. Non-pigmented horn is weak and brittle, and grows slowly. Such feet are always a source of trouble.

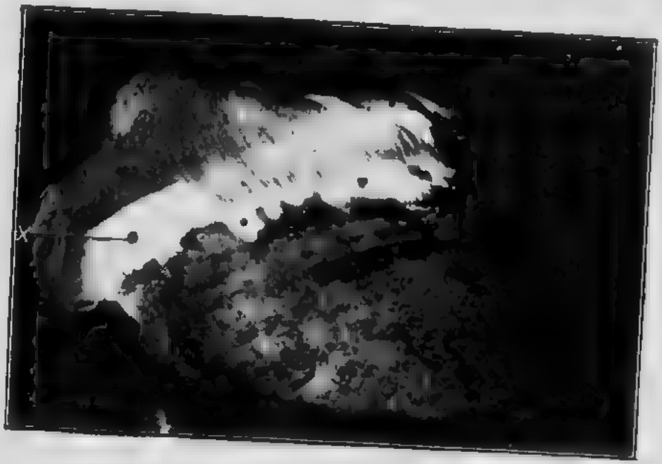

Fig. 135.—The External Foot or Hoof.

The fibrous appearance of the wall may be seen, also the *periople* marked **x**; the hair of the edge of the coronet is clipped away to show this band of white horn, which for the purpose of the photograph was swollen by immersion in water.

The wall is thickest and longest at the toe, thinnest and shortest at the heel. A gradual decrease in thickness occurs from front to rear, but if a section of the wall be made in the direction of its fibres, it will be found that whatever the thickness may be at that particular part, this thickness is maintained from the coronet to the ground surface. The greater thickness of the wall at the toe and quarters as compared with the heels, is connected with the wear and tear of the hoof, and the movements which the latter undergoes under the influence of the body weight. If the wall were as thick at the heels as at the toe it would have been a rigid box; we shall have to show that it is a yielding box, and that the yielding which occurs corresponds to the thin wall of the heels. The reason why the wall is thick at the toe is that this is the region of the greatest friction. The wall at the heels is suddenly inflected, running under the foot in a forward direction for a short distance, and forming an acute angle with the wall. This inflected portion of the wall is called the **Bars**, and in the gap formed by the inflection is lodged the foot-pad. Thus the wall is an incomplete circle of horn, the circle being broken at the posterior part of the foot, and the piece of wall which might have completed the circle is sharply bent on itself and caused to run in practically the opposite direction. When we consider this arrangement it is easy to see the advantages gained by it; the foot is not a rigid body but a yielding one. It would be difficult to understand how any lateral movement could take place had the wall been a complete circle. The value of the inflected portion of the wall is rendered evident when we bear in mind the lateral movement of the foot. From their position the bars afford additional strength; they knit the structures together at the heel in a remarkable way, and prevent any rupture between the wall and foot-pad during the lateral movements of the foot, such as would undoubtedly have occurred had the wall and foot-pad been directly united.

The hind feet differ from the fore feet in shape, being more upright and narrower.

On examining the inside of the hoof-wall a very complex arrangement presents itself. At the upper edge, corresponding to the coronet, is a deep semicircular groove, deepest at the toe and narrowest at the heels, in which is lodged the thick welt of tissue previously described as the wall-secreting substance. Covering the entire surface of this groove are innumerable pin-point holes, into which, as may easily be seen, the papillæ which project from the 'substance' are lodged. The thickness of the wall at any one place corresponds to this coronary substance, and from it the entire horn wall is secreted. The most perfect contact exists between the wall-secreting substance and the groove in which it is lodged, and this contact is further assisted by the vascular papillæ which run for a short distance into the depths of the horn wall.

Horn Laminæ.—On the inside of the wall of the hoof a number of leaves are found arranged side by side, running all round the foot from heel to heel, and composed of delicate plates of horn. It is easy to see that they correspond in size, direction, and length, with the vascular or sensitive laminæ previously described, and like them they possess secondary horn laminæ or lamellæ. These insensitive and sensitive laminæ are arranged towards each other in a peculiar way, by which an enormous amount of strength is obtained, viz., by the process of dovetailing. Each insensitive lamina fits in between two sensitive laminæ, and so powerful is this union, that in endeavouring to separate them the vascular laminæ will often tear from the pedal bone rather than rupture the dovetail. In this way the most intimate and perfect union between the vascular and horn wall is brought about, and in addition other advantages are obtained which will be dealt with shortly. The horn laminæ as their name implies are composed of horn, but the secondary laminæ which invest them are composed of cells which are a something between horn and epithelium, viz., the cells have not undergone a true horn conversion but remain protoplasmic in nature; this is recognised by the fact that they readily stain with carmine whereas horn does not. If our description has been clear, it will be observed that though the sensitive and insensitive laminæ dovetail yet they are never in actual contact, for between them are the lamellæ, both sensitive and insensitive, and it is actually through these structures that the intimate union is maintained (Fig. 133, *d*).

It will be remembered in speaking of the vascular laminæ that we described some as being found beneath the foot; in the same way horn laminæ corresponding in position and number to these are also found under the foot, and are situated at that part which has been described as the bars. Clearly, therefore, the bars, though situated under the foot at its posterior part, are a part of the wall, inasmuch as they possess all the essential anatomical elements of the wall proper.

The **Sole** of every normal foot is concave, that of the hind feet being more concave than of the fore. This concavity agrees with the concavity of the solar surface of the pedal bone, which in itself is ample evidence that the general surface of the sole is not intended to bear weight. Soles vary in thickness, some being very rigid and firm, others very thin and yielding; the sole cannot be too thick. The one shown in Fig. 131 is an excellent specimen of a good sole. The growth of the sole is peculiar; in exactly the same way as noticed in the wall, the papillæ from the vascular sole fit into pin-point holes in the horn sole, and horn is developed around them. But here the resemblance ends; while the horn of the wall is capable of growing to almost any length, until in fact it curls like a ram's horn, the horn of the sole can only grow a very short distance before the fibres break off, and scales or flakes of horn are the result; these either fall out or are pulled out. In other words, the foot determines for itself how thick the sole shall be, and without any assistance the fibres break off when the proper thickness has been attained, and allow the part to drop out This shelling out of the sole is advantageous in th shod foot, inasmuch as the part not being exposed t friction cannot wear away. In parts of the foot such a the wall, which in the unshod foot are exposed to friction no breaking off of horn fibres is required, as the wear an tear maintain the part at its proper length and thicknes The union between the vascular and horn sole is brough about by the papillæ on the surface of the former. The extraordinary length and number of these can only be appreciated by examining the sensitive sole under water.

The sole and wall are united, the place of union being marked by a white line which extends around the complete circumference of the hoof (Fig. 181). That part of the sole situated just within the white line is capable of bearing weight, inasmuch as it is not immediately under the vascular sole. The arrangement of horn at the junction of the wall and sole is peculiar. It will be remembered that the horn laminæ have on them secondary laminæ: these secondary laminæ exist wherever the sensitive horn laminæ digitate. But in the horn of the line of junction of the wall and sole there are obviously no sensitive laminæ, and though the horn laminæ are there and can be distinctly seen with the naked eye, there are no traces of secondary laminæ on them; these have been left behind in the sensitive foot as the wall grows down. The horn formed between the junction of the wall and sole is softer than that of any other part of these two structures; this softness allows of a slight yielding of the sole in an up and down direction, and this we shall find actually occurs.

The **Foot-pad*** or 'frog,' as it is vulgarly known, is a pyramidal-shaped piece of horn, accurately moulded over the plantar cushion, and filling up the space left by the inflection of the wall at the posterior part of the foot. In the foot-pad we meet for the first time with a peculiar soft elastic horn, possessing something of the characters and appearance of indiarubber; nothing in its microscopical appearance accounts for this physical difference in the horn of the pad as compared with that of the wall. Chemistry, however, comes to our assistance, and shows that the horn of the pad contains much more moisture than that of any other part of the foot, and it is the moisture which confers on it its peculiar soft pliable condition. The foot-pad grows from the vascular membrane covering the plantar cushion, in the same way as we have already seen it in the wall and sole. At the heels of the foot, where the wall is inflected, the soft horn of the pad not only fills up the gap between them, but plasters over the inflected edge of the wall for some little distance, so that an inspection of the heel gives the impression that the horn found at the posterior part of the hoof is a continuation of the wall. The overgrowth of the foot-pad is provided against by a method which is a combination of that found in the wall and sole, viz., it is cast off after growing to a certain thickness, while the part next the ground is worn away by friction; in consequence, owing to its rubber-like nature, rags of horn along the edges of the foot-pad are a common and natural condition.

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* The term 'Foot-pad' is introduced not only to define the function of the part, but in order to eliminate the senseless language of the stable from scientific discussion. We should have preferred the term 'cushion' to pad, but this would have created confusion with the plantar cushion. Foot 'buffer,' from some points of view would be a better term, but there are also objections to this.

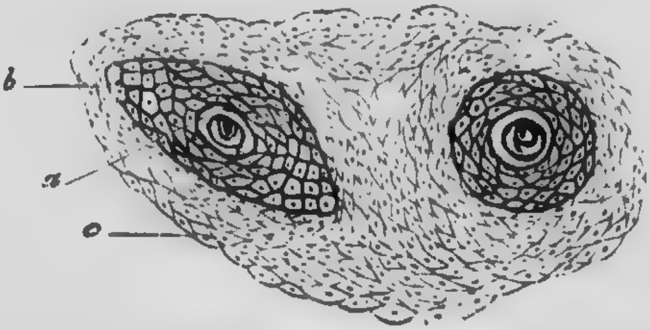

FIG. 186.—HORIZONTAL SECTION OF THE HORN OF THE WALL, HIGHLY MAGNIFIED.

a, Horn tube, a canal containing cellular elements ; *b*, the tubular horn, that is, the horn secreted from the papillæ, forming an oval or circular nest of cells around the canal ; *c*, the intertubular horn.

The Structure of Horn. The horn of the foot consists of epithelial cells which have undergone compression and keratinisation, by which latter process they become hard and tough. It is possible to have horn in the foot which is not keratinised, and the two are very readily distinguished by the process of staining. The double stain picro-carmine has a selective affinity for each kind of horny tissue; the carmine picks out the protoplasmic and non-corneous cells and stains them red, whilst the picric acid stains all tissue which has undergone the process of keratinisation of a yellow colour. By means of this stain we possess a very easy means of determining the character of the horn under examination.

The ultimate horn-cell is a very thin, spindle-shaped, oblong, or irregular body, containing granular matter, a nucleus, and frequently pigment (Fig. 186). In all cases the cells are united at their edges and sides by a cement substance. By acting upon horn with caustic alkalies the cells are in the first instance rendered clear, they then gradually dissolve, are converted into a gelatinous mass and finally they disappear. There is no necessity to use caustic alkali to destroy horn, any alkali has the effect of eroding it. Bearing in mind the highly alkaline nature of the horse's urine, the practical application of this fact in the care and management of the feet is very obvious.

If a portion of horn be examined microscopically, it is found that the compressed epithelial structure is tunnelled in such a way as to form canals or tubes, or, at any rate, to form a structure which is tube-like in nature. These tubes exist wherever the growing surface is invested with papillæ or projections, so that where the papillæ are numerous the tubes are numerous, where they are absent the tubes are absent. The only horny structure not secreted from a papillated surface is the horn laminæ, and here consequently we find no horn tubes, but everywhere else the horn is found to possess a more or less tubular structure. The method of tube formation in horn is very simple; the papillæ growing from the various secreting surfaces are lodged in depressions in the horn, in this way a canal is formed for the reception of the papilla. As the horn grows down from the surface which secretes it, the canal lodging the papilla gradually slides off, but throughout the length of the horn a tubular appearance indicates where the papilla was at one time lodged, and the cells of these tubes from their reaction with carmine prove themselves to be different to true horny structure.

The horn which is secreted in the foot is therefore formed (1) from papillæ found on the secreting surface, and (2) from the spaces between the papillæ. The papillæ form tubular horn, the spaces between them form inter-tubular horn (Fig. 136, b and c). The tube or canal in horn is the outcome of the existence of papillæ; the horn is arranged in an oval or circular manner around the canal (Figs. 133 and 136), the cells composing it being so placed that their edges are towards the papillæ. There is, however, a layer of cells which actually forms the wall of the canal, and these are arranged with their sides next it, or, to put it another way, they stand on their edges. The horn formed by the papillæ is consequently arranged concentrically, and this gives a laminated appearance around the canal, which is best seen in the external and middle layers of the wall (Fig. 136, a, b). In the deep layer of the wall the papillæ produce a much greater secretion, and here the circular or oval masses of cells investing the canal are more prominent, and further, unlike those in the anterior and middle parts of the wall, they need no reagent to identify their cellular nature (Fig. 136, b). If a section of wall be stained with picro-carmine only the canal-contents of the external and middle wall stain with carmine; all the remaining substance takes up the picric acid. In the deep wall this is different; here the whole of the cellular material secreted by the papillæ is stained red, showing that these cells are protoplasmic rather than horny, and partly accounts for the fact that this deep horn is always softer than the middle or external horn of the wall. The horn formed between the papillæ surrounds and knits together that formed by the papillæ. If a section of horn be examined without undergoing any special preparation, it is quite impossible to se the cells of which it is composed; Fig. 133 gives a good ide of this, and represents the fibrous appearance presented b a horizontal section of the wall. To see the cells the preparation has to be treated with a solution of potash o other reagent, when the appearance presented in Fig. 136 is obtained.

At the junction of the wall and the sole the horn of the laminæ is firmly interdigitated with the soft horn of the margin of the sole. This can be perfectly seen microscopically, and further it may be demonstrated that the portion of the sole thus thrust between the horn laminæ is perforated in five or six places for the reception of the papillæ which grow from the inferior extremity of the sensitive laminæ.

If a vertical section of horn be made, we can study the canals now divided in their length. It is readily seen that though spoken of as canals or tubes they are really not empty, but throughout their entire length contain cells which are protoplasmic in nature. These, owing to the manner in which they reflect light, give to the part a beaded appearance. The cells contained within the canal are secreted by the apex of the papilla; they do not fill up the entire lumen of the canal. The use of the canal system in horn is for the purpose of irrigation; the horn must be supplied with moisture, the bulk of this is obtained through these imperfect canals, the soft protoplasmic canal wall readily admitting of transudation. It is not intended to represent that anything like a fluid is

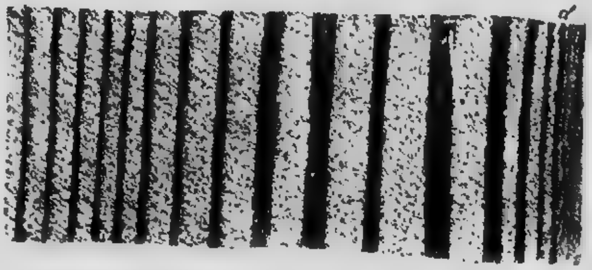

FIG. 137.—MICROSCOPICAL STRUCTURE OF HORN: LONGITUDINAL SECTION OF THE WALL. LOW MAGNIFICATION (AFTER LUNGWITZ).

Note the different size of canals; those on the right are nearest the laminæ; those on the left are towards the outside wall; they are smaller and more numerous than those deeper seated; *d* is a portion of a horn lamina.

circulating along the tubes, but moisture certainly does find its way down, and is readily imbibed by the surrounding cells. Besides this arrangement for maintaining the moisture in horn, there is no doubt that in the intertubular horn moisture passes from the secreting surface from cell to cell, and in this way is transmitted throughout the length of the foot. Constant evaporation is taking place from the foot, and the loss is made good in the manner indicated.

If the invisible moisture which is always escaping from the foot be hindered in its evaporation, the horn becomes sodden, crumbles away, and closely resembles a grey cheese. This experiment can readily be performed on the sole and foot-pad, by accurately moulding to their surface a sheet of gutta-percha and leaving it there. The practical lesson is obvious; no impervious material should be applied to the foot as a protection, or if used it should be ventilated.

Use of the Moisture in Horn.—The amount of moisture contained in horn is something considerable, and the rate at which it evaporates is quite extraordinary. If parings of the foot-pad be enclosed in a bottle, in a short time the interior will become bedewed with moisture. The use of moisture in horn is to keep the foot elastic and so prevent it from becoming brittle. The agency which is at work to prevent the too rapid evaporation of moisture from the wall is the periople, or thin varnish-like layer which covers the wall, and in addition there is the natural hardness of the external fibres of the wall; the latter is sufficient to retain the fibres in their elastic condition by preventing evaporation. In the case of the sole, the layers of exfoliated material which accumulate as the result of the breaking off of the horn fibres prevent undue evaporation. Horn containing but little moisture is in an abnormal condition, it is rigid and brittle; nails driven into the part cause it to crack, and that elasticity on which so largely depends the natural shape and usefulness of the foot becomes impaired, or even destroyed. A museum specimen of a foot will very clearly illustrate our meaning; in its dried condition it is so brittle that if dropped it will occasionally fracture like a piece of glass; but if this foot be placed in water for a few days, it comes out as fresh and elastic as though it had just been removed from the body instead of being probably twenty years old. All that the horn has done is to imbibe water, and the previously brittle substance now becomes yielding and elastic. The entire physiology of the horse's foot is centred around this question of the moisture contained in horn. One of our main objects in shoeing should be to protect the wall from unnecessary interference; the removal of the varnish layer formed by the periople, and the cutting across of some thousands of horn-fibres by the unnecessary use of the rasp, lead to destruction owing to the evaporation of water.

The necessity for elasticity in the foot is evident, when we consider the concussion to which the part is exposed during work, which would inevitably lead to its destruction by fracture or otherwise unless some such provision as this were present. Clinically we are perfectly acquainted with the fractures which occur in the wall of the hoof from violence.

In one part of the foot undoubted evidence of sweat glands exists; these are found in a particular part of the plantar cushion near to and on the sides of the cleft. The glands are very large, coiled, and a spiral duct passes through the horn of the foot-pad and opens on the surface. Fig. 138 is after Franck, who carefully described these structures, though the original discovery was made by Ercolani.*

Chemistry of Horn.—An analysis of the horn of the foot has given us the following results:†

	Wall.	*Sole.*	*Foot-pad.*
Water	24·735	37·065	42·54
Organic matter	74·740	62·600	57·27
Salts	·525	·335	·19
	100·000	100·000	100·00

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* *Veterinary Journal*, vol. i., No. 1.

† 'Chemistry of the Hoof of the Horse,' *Veterinary Journal*, vol. xxv., 1887.

The pad contains the largest amount of moisture, and the wall the least. The salts are small in amount, and consist principally of those of sodium, magnesium, iron and silica, in the form of chlorides, sulphates, and phosphates.

Hoof consists of a horny material or keratin, a substance which replaces the protoplasm originally existing in the cells. Keratin is a proteid-like body found in hair, nails,

FIG. 138.—THE SWEAT GLANDS OF THE PLANTAR CUSHION (FRANCK).

d, *d*, The glands, the corkscrew-like ducts of which (*e*. *e*, *b*) pass out through the horn of the foot-pad, opening at *f f* on to the surfac of the foot. At *c* is the deep-seated portions of the horn of the foot-pad, where it grows from the papillæ of the corium of th plantar cushion ; *g*, *g* are horn tubes seen in longitudinal section.

and even, in a modified form, in the nervous system; i consists of Carbon 51·41, Hydrogen 6·96, Nitrogen 17·46 Oxygen 19·49, and Sulphur 4·23 per cent. The sulphu is loosely combined, and it is this in combination wit hydrogen which causes horn undergoing decay or diseas to have such an offensive odour, sulphuretted hydroge being formed. Keratin is a very insoluble substance, but dissolved by strong and boiling acids and by alkalies. With sulphuric acid it yields leucine, tyrosine, and volatile substances; the latter conferring the peculiar odour on burnt horn, feather, nail, etc.

Provisions for Elasticity and Toughness.—From what we have previously said, it can be seen that it is the wall of the foot which supports the horse's weight. On examining the wall it is found to be thickest at the toe, thinner at the quarters and thinnest at the heels; it is thickest at the toe owing to the wear and tear of the foot at this part. As the pad and posterior part of the foot are the first to make contact with the ground (at any rate in all fast paces),* so the toe is the last part to leave it. The final propulsion being given to the body by the toe, as we have seen in studying locomotion, we can readily understand how necessary it is for this part to be thick and strong. The object of the wall becoming thin towards the posterior part of the foot, is to allow of the elastic movement which we have yet to describe.

Two physical conditions have, therefore, to be provided for in the wall—viz., elasticity of the posterior part, and toughness of the anterior portion. The first is provided by the wall being thinner at the heels than elsewhere; but besides being thinner, the wall of the heel contains more moisture than the wall of the toe, and this moisture ensures its elasticity. The younger the horn, viz., the nearer to the coronet at which it is examined, the more moisture it contains; the further away from the coronet the less moisture, the tougher and more resisting the horn.

The wall grows evenly from the coronet all the way round; if it grows half an inch in the month at the toe, it grows the same length at the quarters, and the same at the heels. The anterior part of the wall is longer than the posterior, therefore the anterior is tougher than the posterior, for the reason that the horn is much older at the extremity of the toe than it is at the heel, and being further away from the coronet, it contains less moisture. The wall at the heel is some months younger than that at the toe; it is thinner, and contains more moisture, therefore it is more elastic but not so tough.

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* Fifty years ago Mr. J. Irvine Lupton communicated a paper on 'Physiological Reflections on the Position assumed by the Fore Foot of the Horse in the Varied Movements of the Limbs,' *Veterinarian*, vol. xxi., 1858. In this communication he states that the heel comes to the ground before the toe; further, he clearly describes the use of the foot-pad, the expansion of the foot, and the final propulsion given by the toe. Mr. Lupton's advanced views did not meet with approval at the time; to-day they are accepted facts.

The age of the wall is an important factor in the wear of the foot. If it takes from nine to twelve months for the wall to grow from the coronet to the toe, the piece of wall at *f*, Fig. 139, is, say, twelve months old, whilst that at *a′* is less than six months old. The horn of the quarter is older than the horn of the heel, and the horn of the toe older than that of the quarter. This excellent provision admits in the unshod foot of considerable friction occurring at the toe without producing undue wear, for the part is hard and tough, while the younger and moister horn at the posterior part of the foot allows of expansion. In this way varying degrees of toughness and elasticity are provided in the wall.

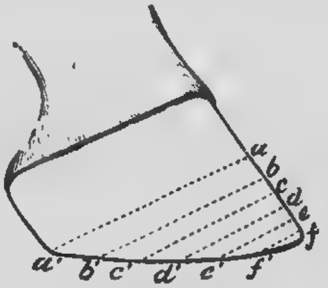

FIG. 139.—DIAGRAM ILLUSTRATING THE AGE OF THE WALL.

a, *b*, *c*, *d*, *e*, *f*, are circles drawn round the hoof parallel to the coronet; in this way it is ascertained that the age of the wall at *a* is the same as the heel at *a′*, the age of the wall at *d* corresponds with the age of the quarter at *d′*. Every portion of the ground surface of the wall is of a different age, being oldest and hardest at *f′*, and youngest and most elastic at *a′*.

The toe of the wall appears to grow faster than either the quarters or the heels, but this is more imaginary than real; it is the tendency of the foot to grow *forward* as well as downward which produces the illusion. That the foot does grow forward may readily be determined by experiment, for if we cut or saw a groove in the wall at the coronet, say an inch or so from the heels, the groove will in course of time be carried some considerable distance towards the toe; the exact amount can be determined by observing the obliquity of the horn fibres.

How the Weight is carried by the Foot.—It is universally recognised that the weight of the body is supported by the union of the insensitive with the sensitive laminæ. That the enormous weight of the horse's body should be carried upon—or, rather, slung upon—thin delicate strips of sensitive material on the one hand, and correspondingly delicate strips of horn on the other, is perhaps the most remarkable feature in the physiology of the foot. We know how firm this union is, the extreme difficulty in a state of health in separating the two surfaces, even by mechanical means, while the structurally delicate nature of the parts yielding this firm connection we have previously considered.

In one foot the weight is carried on 600 or more primary laminæ, and 72,000 or more secondary laminæ. Those laminæ situated at the anterior part of the foot are exposed to more strain than those posteriorly placed, for the reason that they are longer, and they have no plantar cushion and foot-pad to assist them as the shorter posteriorly-placed laminæ have. Moreover, during progression, the final propulsion of the toe comes entirely on them. The short posteriorly-placed laminæ have their strength increased by the direction in which the weight of the body comes upon them. Instead of bearing the weight on the length of the laminæ, as at the toe, they carry it on the side, in such a manner that where we have, say, one lamina at the toe, there are twenty at the quarter. It is not possible to describe this condition clearly, but Fig. 140 will help to explain it.

It will be remembered that the laminæ are attached

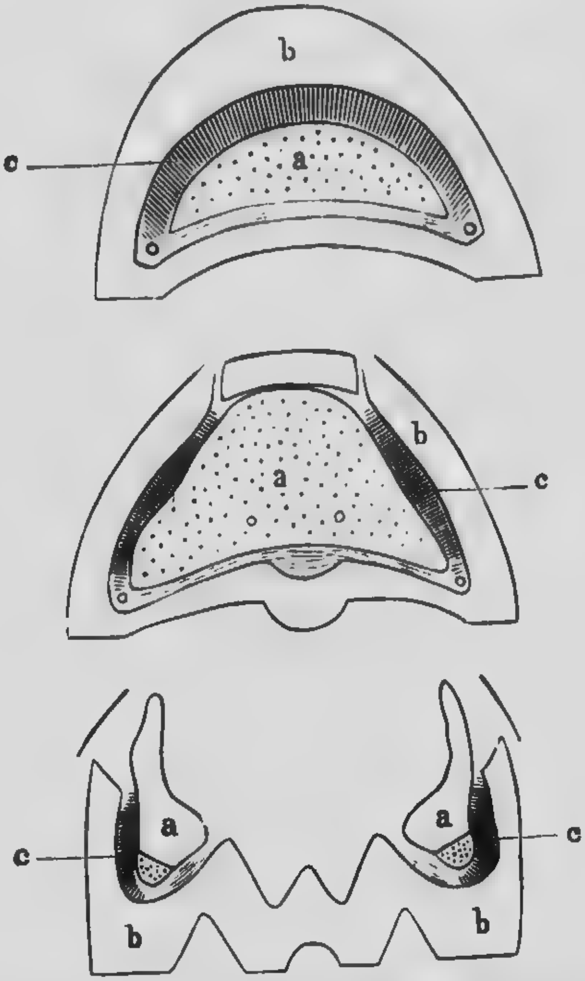

FIG. 140.—DIAGRAMS TO ILLUSTRATE THE DIRECTION TAKEN BY THE LAMINÆ AT DIFFERENT PARTS OF THE FOOT, AS SEEN IN TRANSVERSE SECTION.

In the upper figure the section is made through the toe of the foot: a, being part of the pedal bone; b, the horn wall; c, the laminæ, the latter are practically straight, the weight being imposed from top to bottom in their length. The middle figure is a vertical section just behind the point of the foot-pad: the laminæ, c, give the appearance of being placed above one another. The lower figure is a vertical section through the posterior part of the foot: a, being the lateral cartilage, and c, the laminæ. It will be observed that the laminæ, as in the previous figure, are placed one above the other; this arrangement gives strength, and is a compensation for shortness.

at the anterior and part of the lateral face of the foot to bone, but for the remaining lateral face and posterior part of the foot they are attached to stout cartilage;* if a line be drawn through the foot separating the osseous attachment of the laminæ from the cartilaginous attachment (see Fig. 141), it will be found that, roughly speaking, one-half is cartilaginous and one-half osseous; the cartilaginous portion is situated just where elasticity is required, viz., the posterior face of the wall. One function of the lateral cartilages of the foot is to afford a movable wall-attachment to the sensitive laminæ, and enable them to be carried outwards during expansion. A knowledge of the relation of the posterior laminæ to the lateral cartilage explains the cause of lameness in 'side-bone,' viz., the squeezing of the sensitive laminæ between the wall on the one hand, and the ossifying cartilage on the other.

The folding up of the horn and sensitive leaves in the foot, in the manner above described, has another function besides that of merely supporting the weight and rendering the union firm. The first thing which strikes one in connection with the foot is its remarkably small size in proportion to the size of the body. Comparing the horse's foot, so far as size is concerned, with the human foot, the advantage in the majority of cases lies on the side of the biped. The most interesting fact which physiology has to demonstrate is that, though the foot presents a small circumference, in reality it encloses a vast area due to the anatomical arrangement of the laminæ. It is clear that by folding up this amount of material the surface of the foot is considerably increased. In other words, by this arrangement the foot has been kept within small proportions without affecting its strength. A book, say of 600 pages, may, by placing one leaf on the other, be made to occupy a bulk represented by a few inches; but if each page be laid out separately on the ground, and made to touch the others, the surface covered will be considerable. This is exactly what occurs in the foot, the insensitive and sensitive leaves by their singular arrangement increase the surface of the foot, and yet keep it within reasonable limits. Bracy Clarke, who first had a calculation made as to the increased surface afforded by this arrangement, came to the conclusion that it was equal to 1½ square feet; but Moeller* has estimated that it is equivalent to 8 square feet, whilst Gader's estimate† is 10¼ square feet. For safety we adopt Moeller's number. The bearing surface afforded by each foot is equivalent to 8 square feet, giving a total area of 32 square feet; but it is evident that as feet vary greatly in size, this surface must be greater or less depending on the size of the foot.

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* Some of the laminæ are attached to the tendon of the extensor pedis and the lateral ligaments of the foot-joint.

The physiological function of the leaves of the foot is demonstrated by pathological observation. Inflammation of the laminæ occurs either through overwork, or through an animal standing too long in one position; in either case the parts get strained, and resent it. The practical value of exercising horses which from any reason have to stand for a length of time is well known; the exercise overcomes the tendency of the laminæ to congestion from continual strain, and the feet not only become cool, but the animal may continue standing for a considerable time if exercised daily. The treatment of laminitis by exercise, first taught by Broad, of Bath, possesses a sound physiological basis. If any doubt exists as to the function of the laminæ in supporting the weight of the horse's body, we have only to look at the processes which occur in them as the result of disease. Laminitis is often attended by separation of the horn and sensitive laminæ, when the horse's weight being no longer properly supported, the pedal bone under its influence is actually forced through the sole of the foot.

The Origin of the Horn Laminæ.—No one doubts that the wall grows from the coronet, but great controversy has taken place over the origin of the horn laminæ, some saying they grow like the wall from a part of the coronary cushion, and others affirming that they obtain their origin from the sensitive laminæ. If we were to judge solely by the result of pathological processes, we should be inclined to say the sensitive secreted the horn laminæ; but Moeller* points out that the sensitive and insensitive laminæ are never in actual contact, and that between them are placed the secondary laminæ both vascular and horny. Therefore he argues, and with great weight, that the vascular cannot secrete the horn laminæ, but that the secondary vascular secrete the secondary horn laminæ. If a portion of wall be removed experimentally and the vascular laminæ be exposed, in the course of a short time the part becomes covered with a layer of horn, and this has been used as a strong argument in favour of the secretion of horn from sensitive laminæ; but the horn which is thus secreted is derived from the secondary vascular laminæ, and no one contends that these secrete the primary horn laminæ. The following explanation appears to us to be the correct one: The horn laminæ are secreted from the lower edge of the coronary substance, here white protoplasmic cells are poured out between the papillæ: these cells are carried down with the wall, being pressed into and moulded between the sensitive leaves, thus becoming horn laminæ, the exact counterpart in shape of the mould in which they are made. All this occurs in the region marked 3, Fig. 132. As the wall grows down the horn-leaves are carried with it, so that there is a perpetual movement occurring between the slowly travelling insensitive and the fixed vascular laminæ. The rate of this movement is probably about ·0125 inch in twenty-four hours, on the assumption that the wall grows $\frac{3}{8}$ of an inch in the month. During the time the horny are gliding through the sensitive leaves the vascular lamellæ furnish them with horny lamellæ; and, as we have previously seen, when the wall reaches the sole the horny lamellæ are left behind, while the laminæ emerge with the wall destitute of these structures.

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* *Veterinary Journal*, vol. v.

† Quoted by Goubaux and Barriere, 'Exterior of the Horse' (translation).

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* *Op. cit.*

The Use of the Bars.—The inflected portion of the wall, known as the 'Bars,' runs, as we have previously mentioned, forwards under the foot instead of completing the circle of the wall. The object of turning aside from completing the ring the wall originally looked like forming, is to make room for the elastic posterior foot, viz., the plantar cushion and foot-pad; and the explanation why the wall is turned in instead of ending abruptly, is to afford a solid bearing to the posterior part of the foot, to give additional strength, and to secure a more intimate union with the sole. The bars being part of the wall are intended to bear weight; in the foot of the wild horse and zebra, they present the most extraordinary development as the result of weight-bearing.

The **Use of the Sole** is quite clear, it is to afford protection to the sensitive parts above. Its normally concave shape (Figs. 131 and 140) proves that it is not intended to bear on the ground over its general surface, and the acute lameness which results from a stone in the foot gives further proof, if any were required, of its indifferent weight-supporting properties; that margin, however, in contact with the wall can bear weight. Under the influence of the body-weight the sole becomes slightly flatter, especially that portion of it situated posteriorly, the horns of the crescent. When we come to study the expansion of the foot the object of this flattening will be more apparent. The sole grows from the sensitive sole, as previously described.

The Use of the Foot-pad.—This is one of the chief anti-concussion mechanisms in the foot; it is there to break the jar, and it does so by receiving, in conjunction with the posterior wall, the impact of the foot on coming to the ground; this is imparted to the plantar cushion, and through the lateral cartilages to the wall of the foot, which bulges, or, as it is termed, expands. In breaking the jar (not only to the foot but to the whole limb), it is assisted by its elastic rubber-like nature. The foot-pad needs for its perfectly healthy condition contact with the ground; it is strange that in this respect two structures situated side by side, viz., the sole and pad, should be so opposed in function. We know practically that if the latter be kept off the ground the part atrophies, the heels contract, the foot is rendered smaller, and the pad becomes diseased. This wasted condition of the pad and narrow foot may be restored by pressure, but that pressure must be ground pressure. It is possible by means of a bar-shoe to throw considerable pressure on the pad and heels, but the foot still contracts: it is only when the pad is bearing on the ground that it continues in a healthy condition, and retains its normal size. Foot-pad pressure is, therefore, one of the rules in shoeing if the part is to be able to exercise its natural functions.

The Lateral Cartilages.—We have dealt with certain functions of the lateral cartilages, but it will not be amiss to summarise our knowledge of their use.

1. They form an elastic wall to the sensitive foot, and afford attachment to the vascular laminæ.

2. As the foot increases in width (expansion), the cartilages carry outwards the sensitive laminæ which are attached to them, and so prevent any disturbance of the union of the insensitive and sensitive laminæ.

3. Large venous trunks pass through and close to the cartilages of the foot, and the movements of the cartilages assist the venous circulation.

4. The object of having lateral cartilages in the foot is to admit of expansion under the influence of the body-weight. This increase in the width of the foot is brought about by pressure on the pad, which widens and presses on the bars at H, Fig. 141, and at the same time tends to flatten the plantar cushion, both of which factors force the cartilages slightly outwards. When the posterior wall retracts the cartilages are carried back to their original position. Should this elastic cartilage under pathological conditions become converted into bone, its functions are destroyed, and lameness may occur. By a simple operation relief from this lameness in a large proportion of cases may be secured. It is possible to demonstrate that by

surgical interference the hoof can be made permanently wider, and thereby rendered capable of accommodating lateral cartilages which have undergone an increase in size as the result of ossification. This operation is based on physiological principles.*

Anti-Concussion Mechanism.—Practically the whole physiology of the foot is a consideration of the factors whereby

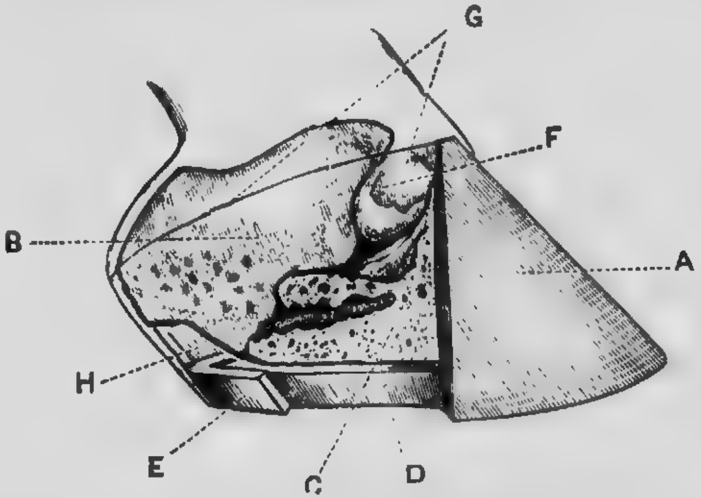

FIG. 141.—PORTION OF THE WALL REMOVED, TO SHOW THE POSITION OF THE RIGID AND ELASTIC SENSITIVE FOOT.

A, Wall of the foot; B, the lateral cartilage; G, a line which represents the coronet; C, the pedal bone—the line of union between the pedal bone and lateral cartilage is well seen; F, is a portion of the corona; D, a portion of the sole exposed by the removal of the wall; E, the heel of the wall left at its plantar surface to show the arrangement of the bar, H, which passes behind and within the lateral cartilage B. The figure, which is accurately drawn from a photograph, is intended to show what an extensive surface the lateral cartilage presents, and the variety of surfaces to which the sensitive laminæ are attached; they cover B, C, and F, the latter in the living animal being the position of the extensor pedis tendon and lateral ligament of the foot, to which the laminæ are attached. Further, the figure shows the division of the internal foot into an elastic and a rigid portion.

the parts are saved from concussion, in spite of wear and tear, batter and jar. The weight carried on each fore foot when the horse is standing is rather more than one quarter the weight of the body; during locomotion the amount varies from half the weight in the trot, to the entire weight in certain stages of the canter and gallop. The mechanisms which exist in the foot to save concussion are not only intended for the protection of the foot but also to save the limb, and they may be tabulated as follows:

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* 'A New Operation for the Cure of Lameness arising from Side-Bones,' *Veterinary Journal*, vol. xxv., 1887.

1. The yielding articulation in the pedal joint.
2. The increase in the width of the foot when the heels come to the ground, known as expansion.
3. The elastic foot-pad.
4. The slight descent of the pedal bone and with it of the sole.

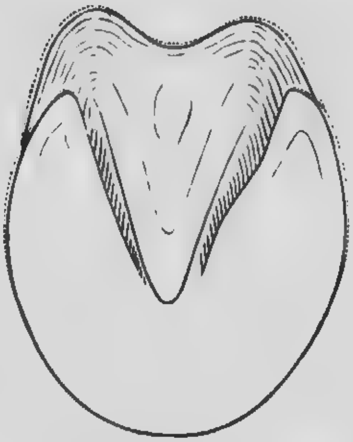

Fig. 142.—Diagram to Illustrate the Expansion of the Foot (Lungwitz).

The unbroken outline illustrates the shape of the foot at rest; the dotted outline shows the portion of the foot which has yielded laterally under the influence of the body-weight.

Expansion.—We have here retained a word warranted by custom though perhaps not free from objection. By its use is indicated the fact that the wall of the foot opposite to the heels becomes wider when the weight comes on this part (Fig. 142). The increase in the width of the foot is not due to a something being added to it, but to an alteration in the shape of certain of its structures; if, therefore, the foot becomes wider it does so at the expense of other parts altering their shape. As a matter of fact an increase in the width of the foot is not the only change which occurs; it can be shown that the heels at the coronary edge sink closer to the ground, while the coronary edge of the wall in line with the toe of the foot retracts, or travels backwards and downwards, Fig. 143, A.

In all fast paces, when the foot comes to the ground, the posterior wall and foot-pad first receive the weight.

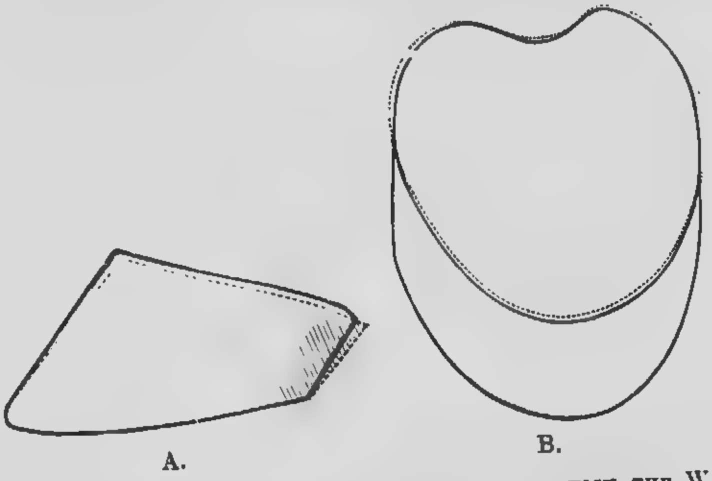

Fig. 143.—Diagrams to show the Area over which the Wall expands, and to illustrate the Retreat of the Anterior Coronary Edge of the Hoof, and the sinking of the Heels (Lungwitz).

A. The unbroken outline shows the shape of the foot with no weight on it; the dotted outline illustrates the retreat of the coronary edge in front and sinking of the heels.
B. In this figure the hoof is looked at from above; the unbroken outline is the coronary edge from heel to heel. The dotted line shows the change in shape it undergoes under the influence of the weight of the body.
In A the shaded part of the wall is to illustrate the area which expands.

Under the influence of the body-weight the foot-pad is compressed and becomes wider, the plantar cushion with which it is closely in contact is also compressed and becomes wider. The effect of this increase in width is that the foot-pad presses on the bars, while the plantar cushion presses on the cartilages, both of which yielding laterally force apart the wall at the heels. When the weight is taken off the foot the heels return to their original position, and the foot becomes narrower. The increase in width which the foot undergoes is something very small; this is probably the reason why for years it has never been accepted as a fact, and that in this country in particular few were found who gave the theory any support.* The employment of delicate apparatus such as that used by Lungwitz† and others, and experimenting upon feet which have not been mutilated in shoeing, have placed the question beyond all doubt.

The area over which the wall expands can be seen in Fig. 143, A; the shaded portion of the heel represents the part which yields laterally. At times expansion is obtained at the coronet and little or none on the ground surface, but as a rule the amount obtained at the coronet can also be obtained near the ground. As to the amount of expansion no definite statement can be made, it is small but is influenced by the shape of the foot; horses with low heels and full well-developed foot-pads register a larger amount than where the heels are high and rigid. The measurements obtained by us with very delicate apparatus were smaller than those obtained in Germany by Lungwitz. On an average we obtained, by simply lifting up one fore-foot, and so causing the horse to throw double weight on the other limb, an expansion of $\frac{1}{50}$ of an inch for half the foot, or $\frac{1}{25}$ of an inch total increase in width. Doubtless during locomotion a greater expansion than this occurs. The question may be asked what advantage can be gained by such a small increase in the width of the foot? Small as the increase is, it still makes all the difference between a yielding and an unyielding block of horn being brought to the ground; it 'gives' instead of offering resistance, and this 'give' is sufficient to prevent the hoof from being fractured, while the pad which has largely caused the expansion has acted as a buffer and assisted to destroy concussion.

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* See footnote, p. 559.

† *The Journal of Comparative Pathology and Therapeutics*, vol. iv., 3.

There is no point in the physiology of the foot which has given rise to greater discussion than the question of expansion, but we submit that its existence is not only proved, but that it is provided for by the anatomical construction of the part and the elastic nature of horn.

The retraction of the coronary edge of the foot in front, and the sinking behind (see Fig. 148), are accompanied by a tense condition of the coronary substance which Lungwitz describes as an elastic ring. Macdonald* in this country regards it as a hydraulic ligament which supports the pedal-joint under the strain to which it is exposed. The view we hold is that the tense state of the coronary substance is due to the alteration in the shape of the coronary edge of the foot, and that the value or existence of any hydraulic support in connection with the joint has yet to be demonstrated.

In addition to the changes in the coronary edge of the foot during the period of expansion, another condition is present, viz., a *compression* of the wall under the influence of the body-weight, which produces a diminution in its height. This can be roughly demonstrated in the following manner: If a portion of the wall, say between the heel and quarter, be cut away so as just to clear the shoe when the latter is fitted, it will be found on placing weight on the limb by lifting up the opposite fore-foot, that the wall has now descended sufficiently to touch the shoe. The only explanation which can be afforded is that given above viz., the wall has undergone sufficient compression t allow the part which was originally clear of the shoe t come in contact with it, and to produce this it must hav diminished in height.

The **Descent of the Pedal Bone** is the last factor employe in saving concussion, and the existence of this has been a strenuously denied as the expansion of the wall; there i however, no difficulty in demonstrating it, and we can readil see the value of this function. Concussion to the sensitiv foot is prevented by a slight up-and-down play between th sub-laminal tissue and the pedal bone; as the weight comes on to the foot the pedal bone descends slightly, to rise again when the weight is taken off it. As the pedal bone descends, the horn sole on which it is resting also slightly descends and comes nearer to the ground; this is one reason why the sole is concave instead of flat. The descent of the internal foot saves concussion, in the same way that it is easier to catch a cricket-ball with a retreating movement of the hand than by rigid opposition; further it facilitates the circulation. The descent of the pedal bone is a most important physiological factor and one of the safeguards of the sensitive foot.

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* *Veterinary Record*, No. 145, 1892.

Vascular Mechanism.—Lying as the foot does furthest from the heart, we are led to inquire why it is that the blood is able to circulate through it so thoroughly, and whether other means are at hand for assisting the force of the heart in facilitating the circulation. Such means do exist. Though the contraction of the left ventricle is sufficient under ordinary circumstances to bring the blood back to the right side of the heart from any part of the body (as we have pointed out in dealing with the circulation), it is doubtful whether it would be wholly sufficient to empty the foot of blood or keep the considerable plexus of veins full. This plexus is shown in Fig. 134, p. 546, which is a reproduction from a photograph of a corrosion injection.* The figure conveys very accurately an idea of the remarkable venous arrangement of the foot.

The venous circulation is assisted by two movements in the foot, viz., the expansion and recoil of the outer foot, and the descent and elevation of the inner foot. There is no difficulty in seeing the movement imparted to a column of fluid circulating in these parts, for if a plantar vein be divided and the horse made to walk, every time the foot comes to the ground the blood spurts out from the vein as if from an artery; when the foot is taken off the ground the stream of blood becomes greatly reduced. A perfect pumping action is in this way produced. The mechanism can also be demonstrated on the dead limb, by placing a manometer tube filled with water in each plantar vein, and then pressing downward on the limb, thus roughly imitating the weight on the leg. With every compression of the foot the water rises in the manometer tube, and falls during the period of no pressure, a period corresponding in the living animal to the foot being off the ground.

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* The figure appeared in an article by Dr. C. Storch, of Vienna, on 'The Venous System of the Horse's Foot,' *Oesterreichischen Monatschrift für Thierheilkunde*, 1898.

We must accept it, therefore, as a proved fact that the venous circulation is largely facilitated by the expansion and contraction of the posterior part of the foot; during expansion the blood is being driven upwards, and during recoil the veins aspirate the blood into their interior. Indeed, so perfect are these mechanisms that, as previously pointed out, there are no valves in the veins of the foot, and none are found nearer than the middle of the pastern. To assist the circulation, the large venous trunks at the postero-lateral part of the foot are in close connection with the lateral cartilages, and some of the vessels even pass through their substance.

In conclusion we may with advantage summarise what has been said about the anti-concussion mechanisms:

When the weight comes on to the foot, it is received by a yielding foot-articulation, an elastic wall, bars and pad, and through these by the plantar cushion. The elastic posterior wall is pressed outwards by the compressed indiarubber-like pad and plantar cushion, and it expands slightly from the ground surface to the coronet. At the moment of expansion, the bulbs of the heel of the foot at the coronary edge sink under the body-weight and come nearer the ground, and as a result of this the anterior coronary edge retracts. The pedal bone descends slightly through its connection with the sensitive laminæ, and presses the sole down with it, while the wall of the foot diminishes in height under the compression to which it is exposed. Under these conditions the blood-pressure in the veins of the foot rises, and the vessels are emptied. When the weight is removed from the foot the bloodvessels fill, the pad and posterior walls recoil, the bulbs of the heel rise, and the foot becomes narrower from side to side; at the same time the anterior edge of the coronet goes forward, and the pedal bone and sole ascend.

Such are the physiological features of the foot which facilitate the circulation and help to counteract concussion. Foot-lameness is only too frequent, but if it were not for the mechanisms we have described, it would not be possible for horses to work for a single day.

Physiological Shoeing.—It is impossible to conclude this chapter on the foot without some mention of what might be termed physiological shoeing.

We all recognise the evils of shoeing as strongly as we realise its necessity. By bearing in mind the functions of the various parts of the foot, we can certainly reduce these evils to comparatively narrow limits. The following rules form the basis of physiological shoeing:

1. The reduction of the wall to its proper proportions, such as would have occurred through friction had no shoe been worn.

2 Fitting the shoe accurately to the outline of the foot, and not rasping away the exterior of the crust to fit the shoe, since this not only renders the horn brittle, but is so much loss of bearing surface.

3. The exterior of the wall should be left intact. The practice of rasping the wall for the *sake of appearance* destroys the horn, and allows of such considerable evaporation from the surface of the foot that the part becomes brittle.

4. The sole should not be touched with the knife; it cannot be too thick, as it is there for the purpose of protection.

5. The bars should not be cut away, they are part of the wall, and intended to carry weight. The shoe should rest on them.

6. The foot-pad should not be cut, but left to attain its full growth. No foot-pad can perform its functions *unless on a level with the ground surface of the shoe.*

7. The pattern of shoe is immaterial so long as it has a true and level bearing, and rests well and firmly on the wall and bars. We believe, the simpler the shoe the better, viz., one flat on both ground and foot surface. It should be secured with no more nails than are absolutely necessary, as the nails destroy the horn; further, the nails should not be driven higher than needful, for high nailing is ruinous to feet.

Such, briefly, are the conditions which fulfil physiological shoeing.

Pathological.

No useful summary of foot trouble can be given. Practically every structure in it is liable to disorder. It is the most common seat of incurable lameness, and has always been so since the horse was subjected. 'No foot, no horse' is as old as the days of Xenophon. This horsemaster tells us how to keep the horn of the feet of cavalry horses hard —a very necessary matter at a time when shoes were unknown. It is a remarkable fact that the horn of unshod feet is infinitely harder than that of horses wearing shoes. The wall may be so hard as even to resist a nail being driven in.

CHAPTER XVIII

GENERATION AND DEVELOPMENT

THE **Sexual Season** of animals is a subject which in recent years has received exact expression at the hands of Heape,* whose communication, quoted below, we have followed in connection with this question. Heape divides female mammals into two classes, *Monœstrous*, or those which have one œstrous cycle, and *Polyœstrous*, or those having a series of œstrous cycles. The first phase of generative activity at the beginning of a sexual season is known as *Proœstrum*, or the *Proœstrous period*; it corresponds to the period 'coming on heat,' or 'coming in season.' The period lasts a variable time in different animals, and is succeeded by the *period of desire* or *Œstrus*; it is only during this period that sexual intercourse is permitted, or that fruitful coition is possible. If conception does not occur or is prevented, œstrus is followed by *Metœstrum*, or the *metœstrous period*, during which sexual activity passes away, and is succeeded by a period of complete rest or freedom from sexual excitement known as *Anœstrum*. The anœstrous period may last two, three, eleven, or more months depending on the species.

The sexual cycle is not always as above described; there are animals in which metœstrum is not followed by a period of complete rest, but by a short quiescence known as *Diœstrum*, which lasts a certain number of days, and is then followed by a new proœstrum, œstrus, metœstrum, and diœstrum.

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* 'The Sexual Season of Mammals,' etc., by W. Heape, M.A., *Quarterly Journal of Microscopical Science*, vol. xliv., p. 1, 1901.

Among monœstrous mammals is the wolf, which in the wild state has only one sexual season in the year; another is the dog, though in this case the sexual season may recur during the year, but the periods in each case are quite distinct, and followed by complete rest, which is the essentially distinguishing feature. Among polyœstrous mammals are the mare, cow, sheep, pig, and all of these during a portion of the year exhibit a series of diœstrous cycles (in the absence of pregnancy), followed by anœstrum until the next year.

The number of annual sexual cycles which any given species passes through is vastly influenced by domestication. Probably in all primitive species one sexual season yearly was the rule. Domestication alters this. The abundant food supply renders the struggle for existence no longer acute, the dread of being preyed upon by the enemies peculiar to each species is removed, and one of the responses to these altered conditions is a greater desire to multiply, for the reason that the energies previously expended in the struggle for life are turned into a fresh channel. The cat in a wild state has one sexual period a year, the domestic variety has three or four. The wild dog and wolf breed once annually, in captivity twice annually. The lioness in a wild state has probably but a single breeding season, in captivity the œstrous period may be three or four times a year. Bears in a wild state have a single breeding season, in captivity more than one. The wild otter has a single season, but in a state of captivity she comes 'in season' every month (Marshall and Jolly). So far, in fact, as evidence is available, a single sexual season for animals in a state of freedom appears to be the natural condition, *polyœstrum* being an acquired character. The frequency of œstrus under domestication is essentially influenced by food, temperature, and environment.

The complete œstrous cycle in the *dog** under domestication is six months. Every six months, in spring and autumn, the majority of dogs come 'on heat,' though there are many exceptions to this rule, some of the smaller breed of dogs having a three and four heat period in the year. The period of prœstrum lasts from seven to ten days and œstrus lasts another week.

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* 'Contribution to the Physiology of Mammalian Reproduction.' Part I.: 'The Œstrous Cycle in the Dog.' By F. H. A. Marshall and W. A. Jolly. *Phil. Trans.*, B. vol. 198. 1905.

In the *mare* the complete œstrous cycle with its diœstrous intervals may last for months, in the majority of mares from February to June or July, and unless rendered pregnant the diœstrous periods last twenty-one days, and are followed by prœstrum, œstrus, etc., as previously described, though the time duration of these is irregular, generally brief, and always uncertain. For instance, the exact period at which the mare is ripe to receive the male may only be a matter of a few hours, whereas she may be several days in a highly unsettled sexual condition. The mare is in a condition of œstrus on the seventh to tenth day after foaling, with thoroughbred mares it may be the sixth; at this period, though still nursing, she desires intercourse, and in this respect differs from the nursing cow and sow. If she does not conceive the period of diœstrum is twenty-one days, and followed by œstrus, the returning heat usually lasting longer by two or three days than the original heat.

The *cow* under domestication will breed at any time of the year (Goodall). She ordinarily takes the bull six weeks or two months after calving, but it is unusual for her to accept the bull while suckling her calf. If the latter be removed or weaned she shows signs of œstrus six or seven days later, the duration of which may be twelve hours. The period of diœstrum is twenty-one days, at the end of which time both cows and heifers exhibit œstrus; this cycle continues until they are settled in calf.

With *sheep** œstrus may only last one or two days, or it may pass away very quickly, the diœstrum which follows lasting from thirteen to eighteen days. The number of recurrent periods in any one cycle in the sheep have been observed to depend upon breed; two, three, or four recurrent periods have been noted. There are some breeds of sheep which may produce two sets of lambs in one year. The period of œstrus may be induced almost at any time in the late summer and autumn by the introduction of the ram to the ewes (Goodall).

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* 'The Œstrous Cycle and Function of the Corpus Luteum in the Sheep,' by F. H. A. Marshall, B.A. *Phil. Trans.*, B. vol. 196. 1903.

The *sow* takes the boar about a week after she has weaned her litter, or about eight weeks after farrowing. The period of œstrus lasts about two days, the diœstrous period twenty-one days.

The only known animal which in a wild state exhibits a continuous series of diœstrous cycles is the monkey, but even in this case there is a limited season when conception is possible (Heape).

The œstrous period may appear in the dog after a portion of the spinal cord has been excised, proving that it is a process quite independent of any reflex act, that it may exist in the absence of any knowledge on the part of the animal, and that its production is under no central control. Furthermore, such an animal may become pregnant and be delivered in the ordinary way, though quite unconscious of the process.

The *external signs of proœstrum* in all animals is a swelling of the vulva more or less pronounced, with a slight flow of mucus which may be blood-stained. There is excitement, the mare may refuse to work, squeals and kicks when approached, elevates and protrudes the clitoris, micturates frequently, the material being very mucoid. The cow bellows, is excited, and mounts its fellows. Sheep become restless and follow the ram. The dog is playful, excited, and desires the attention and companionship of the males of her own species. In all animals it is only during the actual period of œstrus or desire that copulation is permitted, and in all polyœstrous domestic animals this period is variable in extent.

Changes in the Uterus during Sexual Excitement.—During proœstrum there is an increase in the uterine stroma, injection of the mucous membrane in consequence of a dilatation of the capillaries, and usually a breaking down of the walls of the latter, leading to extravasation of blood into the stroma, or even into the cavity of the uterus. The glands of the uterus swell and pour out a slight secretion. In some animals such as the monkey the epithelial lining of the uterus is destroyed during this period, but with ungulates desquamation of the uterus is probably very rare, while in carnivores it occurs more or less in every case. The pigmentation found in the mucous membrane of the uterus after œstrus is due to the extravasation of blood; this blood is also the source of the blood-stained discharge, and on a more extensive scale is the cause of the menstrual flow in monkeys and women, in both of which there is in addition blood collected in lacunæ in the wall of the uterus and destruction of the epithelium. Gradually in all animals the uterus recovers its normal appearance, proœstrum passes away, and is followed by œstrus. Bearing in mind the rapidity with which œstrus may follow proœstrum in such animals as the mare, cow, and sheep, it is evident that the whole of the above process cannot always be fully gone through; but in the dog, whose cycle is far more regular, the uterus undergoes the changes described.

By systematically preventing animals from breeding the sexual season may be interfered with to the extent of complete cessation (Heape). Certainly the mare used late in life for breeding purposes often proves barren. Yet there are mares which, though deprived of the services of the male, never lose their desire, and may for the greater part of their life be a source of danger from sexual excitement. The cause of œstrus is an internal secretion produced by the stroma of the ovary. (See *Corpus Luteum*, p. 591.)

When male animals suffer from a periodic sexual excitement it is known as **rutting**. This term should be confined entirely to a male sexual season, such as is experienced by the camel, stag, elephant, and ostrich. In the rutting stag the neck becomes enormously swollen (Leeney), the elephant experiences a discharge from the temporal gland, and the ostrich becomes red in the legs. All these are at this time dangerous to approach, and are frequently violent and aggressive.

Effect of Removal of Testicles and Ovaries.—The influence of the removal of the ovaries and testicles on general metabolism is a subject which has been referred to in dealing with internal secretions (p. 265), and attention was there drawn to the fact that both in cats and dogs the complete removal of the ovaries, and, it may be added, of both horns of the uterus, may not in every case prevent an animal exhibiting œstrus. Such, of course, are exceptional cases, for ovariotomy usually suppresses the function. If an animal, for instance, be operated upon before puberty, viz., before an œstrual period has had time to appear, such an one will not subsequently experience any sexual excitement. If the operation be performed during the first pregnancy, the 'heat' period does not occur. If operated upon after one or more œstrual periods, and not being at the time pregnant, there may be a few returning heat periods and free sexual intercourse.

If castration of the stag be practised the antlers fall off from the seventh to the ninth day after operation; fourteen days is said to be the longest time they remain. This is evidence of an internal secretion of the testicle (p. 265) which influences the growth and shedding of the antlers, while the chain of evidence is completed by the fact that castration on one side only affects the growth of the antler on that side. If the epididymis be left after complete castration, its presence modifies the growth of the next pair of antlers.*

Similarly the growth of parts in other male animals is affected by castration. Cats operated upon while very young have heads which are indistinguishable from the female; the tissues of the jowl, which give the head of the male cat such a massive appearance, are lost after castration, and this may occur even when the operation is performed late in life. Female cats operated upon while young acquire a head of the male type, and even if the operation be performed when approaching middle life, there is a disposition to broadening of the skull (Leeney).

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* I am indebted to Mr. H. Leeney, M.R.C.V.S., Hove, for these facts and much other information on the subject.

The alteration in the shape of the male and female skull observed in the cat when castration or ovariotomy is practised in early life, supports the view advocated by Heape that no being is wholly male or wholly female, but a portion of each sex with one predominant. Cocks converted into capons when young do not develop such full male plumage, and the combs and wattles are more like those of the hen. Pullets from which the 'clutch' has been taken grow fat, and sometimes put on male plumage. Hen pheasants injured by shot in the ovarium have frequently been found with male plumage, and disease of the ovary in hens or pheasants may lead to their crowing (Leeney).

The Testicles are solid organs with an external covering of serous membrane, and possessing a *tunica albuginea*, and a *stroma* or framework of fibrous tissue. The spaces of the meshwork are occupied by the *seminiferous tubules*. These tubules are highly convoluted in the parts immediately concerned in the formation of spermatozoa, and commence usually by blind extremities. If the changes in the cells found on the basement membrane of the tubules be followed, it is found that the cells of the lining epithelium divide into two daughter cells, one remaining attached to the basement membrane, the *sustentacular cell*, the other becomes a *spermatogen*. The spermatogen-cells divide and subdivide to form other cells that are recognised as *spermatoblasts*. These spermatoblasts elongate and pass into *spermatozoa*, collecting into sheaves as they do so, and becoming attached to the sustentacular cells that are placed on the basement membrane. These sustentacular cells minister to the needs of the developing sperms until they are fully matured. The latter are then set free, and pass into the lumen of the tubule. The spermatozoa are produced in enormous numbers; it is estimated in man that each cubic centimetre of seminal fluid contains from sixty to seventy millions of cells.

A mature spermatozoon under favourable conditions is active, moving about rapidly in the seminal fluid by means of its long vibratile tail. It is formed of a head, a middle piece or body, and a tail. The head corresponds to the nucleus, and is constantly present, the middle piece and tail are developed to a varying degree in different animals. In the horse the length of the head, which is bluntly pear-shaped, is about 5 μ,* the tail is eight or nine times as long as the head. It is supposed that the sperm-cell extrudes polar bodies as does the ovum (p. 589), but they have not been recognised. The head of the sperm may be considered as the male pronucleus.

The **Spermatic Fluid** is alkaline or neutral in reaction, of viscid consistence, contains proteids, nuclein, lecithin, cholesterin, fat, leucine, tyrosine, kreatine, inosite, sulphur, alkaline earths, chloride of sodium, and phosphates.

The essential element is the *spermatozoa*, without which the fluid is not fertile. Spermatozoa exhibit spontaneous movement, the long tail moving from side to side, by which means the organism is propelled when placed in the body of the female. The vitality of spermatozoa under suitable conditions is considerable, and when placed in the body of the female they have been found very active many days after copulation. Colin found them active in the vesiculæ seminales eight days after castration. The spermatozoa are readily killed by ordinary or acidulated water, glycerin, etc.

It is not known in what way the secretions of the *prostate* and *seminal vesicles* influence the main secretions with which they are ejected, but it is supposed they maintain the motility of the spermatozoa. The prostatic fluid precedes the spermatic in ejaculation, and in stallions and bulls, when excessive daily demands are made, the fluid ejaculated is largely prostatic and infertile. The testicular products of hybrids, such as the mule, are infertile.

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* μ = a micron; $\frac{1}{1000}$ millimetre = $\frac{1}{25000}$ inch (nearly).

The **Period of Puberty**, or that time in the animal's life when it is capable of procreation, has been put at 1½ years for the horse, 8 to 12 months for bovines, and 6 to 8 months for the sheep, pig, and dog. There is, however, a great difference between capability and *fitness* for procreation. Breeding from immature animals is one explanation of a great deal of the worthless material in the shape of horses which may be seen in all countries.

The advent of maturity is marked by certain changes in form, particularly in horses. They lose their awkwardness, the outline of the frame becomes more consolidated and in greater unison. In the male the neck becomes thick and curved, the voice deepens, and the whole appearance denotes life and vigour. In both the stallion and bull the temper is usually irritable and uncertain, and often extremely vicious. The age at which procreation ceases is not known. Fleming says that mares have been known to produce foals at 28, 32, and 38 years of age, and it is certain that some good stallions have been advanced in years.

The **Act of Erection** is a vascular phenomenon produced by an engorgement of the erectile tissue of the penis with blood. This engorgement is brought about by stimulation of the *nervi erigentes*, which arise from the sacral portion of the cord. These nerves furnish dilator fibres to the vessels of the penis, and under their influence the cavernous spaces of the erectile tissue become gorged with blood under pressure. The nervi erigentes act reflexly through an erection centre in the cord, while the erection centre is under the influence of higher centres in the brain. Erection and ejaculation in the dog may be produced by stimulation of a definite area of the cortex of the cerebrum, and they may also be produced after section of the spinal cord in the lumbar region. The sensory nerves in the penis, by which erotic sensations are carried, are the pudic; if the pudic nerve be cut erection is impossible; if the central cut end be stimulated it leads to ejaculation.

The first portion of the penis which receives the excess of blood in erection is the corpus cavernosum; the spongiosum and glans are not fully erect in the stallion until the penis is introduced into the vagina; at the moment of ejaculation in this animal the glans swells enormously, apparently to cover or grasp the os uteri. Though the organ in the horse assumes such considerable proportions, in the bull this is not marked. The peculiar penis in this animal comes to a narrow point without any of the swelling observable in the stallion. In the act of erection, the S-shaped curve of the penis is removed, and the organ elongates; at the same time the retractor muscles of the sheath draw back the prepuce and the organ is exposed. In the ram, also, the penis is narrow and pointed, and the vermiform appendix at its extremity appears essential for successful impregnation, for if it be removed, it is said the animal proves sterile. In the dog the increase in the size of the penis is mainly at its posterior part, and the bulbous swellings there observable are the portions grasped by the spasm of the sphincter cunni of the female, rendering withdrawal impossible until complete relaxation occurs. The bone in the penis of the dog facilitates its introduction into the vagina.

Sexual Intercourse.—Copulation is not necessary in all animals, nor indeed in any. What is required is merely an interchange of elements from the nucleus of two different cells. To this last statement a slight exception might be taken, because there is a condition, *parthenogenesis*, where the access of a second element is not required, but this method of development is unknown in the higher animals. The act of intercourse is of short duration in the majority of animals, excepting the dog, pig, and camel. Colin places it at ten to twelve seconds for a vigorous stallion; it is exceedingly rapid, almost instantaneous, in the bull and ram, probably from the peculiar shape of their intromittent organ. The spermatic fluid is forced into the vagina, or even directly into the uterus. The peculiar termination of the urethra of the horse, and the bulbous enlargement of the glans during the final act of coition, point to the organ grasping the os at the moment of ejaculation, while the projecting portion of the urethra is inserted into it, by which means some of the fluid is undoubtedly directly injected into the uterus; the pointed penis of the bull and ram makes it certain that such is also the case in these animals. An examination of the uterus of the sheep and dog a few minutes after coition has revealed the presence within it of spermatozoa. There is ample evidence that the spermatozoa may remain alive for several days within the uterus. At the moment of intercourse the uterus becomes erect, and the introduction of the male element into it is further assisted by the aspiration following its subsidence.

The actual mechanism of ejaculation is produced by a contraction of the vesiculæ seminales, the prostate gland, and probably of the vasa deferentia, through the reflex action of the ejaculation centre in the lumbar and sacral portions of the cord. By this means the seminal fluid is forced out of the vesiculæ into the urethra, and by means of the muscles of the perinæum is forcibly ejected from the urethra. In animals possessing no vesiculæ, such as the dog, ejaculation takes place direct from the testicle and vas deferens.

The Ovaries.—They are solid organs, and about half the size, or a little less than half the size, of the testicle of the male. An exception to this must be made in the case of the sheep; here the ovary is very small compared to the testicle of the ram, this animal for its size having probably the largest of testicles, certainly among the domestic males. The ovaries of the mare, cow, and sheep, are somewhat ovoid with a slight depression termed the hilum; the ovaries of the pig and dog are lobulated and resemble a bunch of grapes; the ovary of the cat and rabbit is more or less lenticular. The substance of the ovary is divided into cortex and medulla: the cortex being that portion containing the developing eggs or ova, the medulla being the solid, connective tissue, vascular core. Covering the ovary is a modified endothelium, the *germinal epithelium.* This is of the columnar type (a modification of the endothelium of the body cavity), and is found over the whole ovary except where the ligament of the ovary passes to the uterine horn, and where the broad ligament of the uterus is attached to the ovary itself. The epithelium is called germinal because from it the eggs are developed during intra-uterine life; it is probable that no new ova are formed after birth. During development the germinal epithelium grows into the body of the ovary as a long cylinder of cells. These cells eventually are cut off from any connection with the epithelium covering the ovary, and one cell, it may be two, takes on the appearance and characters of an ovum. The other cells that have accompanied and been constricted off with the ovum take on the duties of the membrana granulosa, which is merely a cellular sphere containing the ovum. The earliest ova are found in the cortex as large cells enclosed in the simple one-layered *membrana granulosa*.

The changes that occur from this primitive condition until the ovum is mature are chiefly indicated in the wall of the structure containing the egg, the so-called *Graafian follicle*. A connective-tissue capsule, the *tunica fibrosa*, originates around the follicle, and finally a cavity appears owing to a splitting of the membrana, a cavity containing a fluid under pressure, the *liquor folliculi*. The ovum continues to grow slowly until it reaches about $\frac{1}{125}''$ (·18 to ·2 mm.) in diameter, and is found in an upheaval of the cells of the membrana granulosa known as the *discus* or *cumulus proligerus*.

The Graafian follicle of the adult animal consisting of the above-mentioned parts, and containing the ovum, extends throughout the thickness of the cortex of the ovary, and daily becoming larger, it appears eventually as a vesicle on the surface. The formation of the liquor folliculi under pressure, and its tendency to move in the direction of the least resistance, will influence the point of rupture, which is said generally to occur at the hilum or thereabouts.

When rupture of the Graafian follicle occurs the ovum is flushed out, and at the same moment, according to Henson, the fimbriated extremity of the Fallopian tube becoming erect grasps the ovary, and thus the escaping ovum is received into its 'duct.' Probably the converging furrows found on the plicated extremity of the Fallopian tube may assist in directing the ovum to the *ostium abdominale.* If by chance the ovum be not caught and carried away to the uterus as described, it may fall into the peritoneal cavity and perish, or if it has been already fertilized abdominal fœtation may occur, the peritoneum acting as a matrix in which the embryo may develop.

The Ovum.—With the exception of those produced by the *prototheria* (duck-mole and spiny ant-eater), the mammalian ova are extremely small. They vary in size from $\frac{1}{150}$ to $\frac{1}{120}$ of an inch, and although not to be compared to those of birds, reptiles, or amphibians, yet they are undoubtedly the largest cells found in the mammalian body. The greater size of the eggs of birds, reptiles and amphibians is due to the quantity of deutoplasm or yolk contained therein. In mammals this is small in amount, owing to the speedy union of the developing ovum to the uterine wall, which effects an intimate connection with an abundant food supply.

The ovum is a typical cell, it is spherical and more or less translucent. It has a thick cuticle or *zona radiata,* within which lies the protoplasm and vitellus or yolk, confined in a special membrane the *vitelline membrane.* Within the vitellus or yolk is the *germinal vesicle* or the nucleus of the cell, and within this the *germinal spot* or nucleolus. This is the structure of the ovum prior to its extrusion from the Graafian follicle; but either just before or immediately after escape from this, and *prior to impregnation,* changes occur. These changes more especially involve the nucleus or germinal vesicle, and are known as the formation of the polar bodies.

The extrusion of the **Polar Bodies** has been studied by Van Beneden in the ova of the *ascaris megalocephala* of the horse, and what is true of this is believed to be true for the mammalian cell. The first stage is that of indirect division of the nucleus, and its movement towards the periphery of the cell. The nucleolus probably divides in a similar manner, but its fate is not known. The nucleus having divided, one half is extruded into a space beneath the zona radiata; thus the *first polar body* is got rid of. The half of the nucleus still remaining in the ovum divides, and for a second time a nucleus is extruded, forming the *second polar body*.

There have been many explanations offered of the significance of the polar bodies. Two, however, are important and worthy of mention. Minot and Balfour believed that they were intended to prevent parthenogenesis, or the possibility of a new creature developing from an ovum that had never received a male element. Weismann believes that by the loss of certain elements by means of the polar bodies, the ovum is rendered receptive for characters of the male; in other words, it has a bearing upon the hereditary properties of ovum and sperm, the polar bodies carrying away superfluous histological and genetic properties.

As a result of the rupture of the Graafian follicle, a rent is made in the ovary. This wound fills with blood from the opened vessels, and for some time afterwards appears as a pigmented spot. If pregnancy has not supervened, it undergoes a retrogressive metamorphosis and soon disappears. If, however, the ovum is fecundated, the *corpus luteum*, as this pigmented spot is termed, continues to grow, and may be observed in the ovary even near term.

The **Corpus Luteum** of the pregnant animal is very much larger than that of the non-pregnant, and it appears to be conclusively settled that the existence of this yellow tissue in the ovary is not for the mere purpose of filling up a cavity in its structure, but that the yellow body is a ductless gland which becomes an active secreting agent, producing a secretion by which the ovum is anchored to the wall of the uterus, and its nourishment and development assisted. This ductless gland is functional until about the middle of pregnancy, when it is no longer a necessary factor in the nourishment of the embryo and consequently degenerates. That the corpus luteum takes little or no share in the production of seasonal sexual excitement appears quite clear; this is the function of the stroma of the ovary which pours an internal secretion into the blood, and so brings about menstruation and œstrus.

Ovulation is the process of egg extrusion. In some animals, as the rabbit and ferret, it can only occur as the result of coition, the presence of spermatozoa in the uterus being essential to the act. In others, and they represent the majority, such as the mare, donkey, cow, sheep, pig, and dog, ovulation occurs during œstrus, but the act of copulation is not necessary to extrusion, and in such animals artificial insemination* is therefore possible. The period of œstrus is not necessarily identical with the period of ovulation, œstrus may occur without ovulation, and ovulation may occur without œstrus. Ewart says the mare may mature and discharge one or more eggs after she has become impregnated. Ovulation occurs at the moment the Graafian vesicle ruptures and the ovum is ejected. The number of ova which may be extruded during one sexual period is not known with any degree of certainty; in the case of the cat and dog there is evidence of several being ejected, for each fœtus represents a separate egg. The number of eggs laid is always greatly in excess of the number impregnated, and the mare which probably only produces one egg at a time, and with whom twin births are very rare, is believed by Ewart to shed about ten or twenty ova annually. Whether an equal number is discharged by each ovary is unknown. Probably one ovum for the mare, cow, ass, deer, elephant, or monkey at each œstrous period is the rule, though two may be discharged. The sheep probably discharges one to four, the dog, wolf, and cat five to six, the pig ten or even fifteen.

Determination of Sex.—Heape† maintains that there is no such thing as a pure male or female animal, but that all contain a dominant and a recessive sex, excepting hermaphrodites, in which both sexes are equally represented. The assumption of male characteristics in old females, and of female characteristics in old males of the human species, is noted by Heape. We have referred on p. 582 to the remarkable effect of castration and ovariectomy on the skull of young cats, castration producing a female skull, ovariectomy a skull of the male type. Caponning also induces female plumage. Injuries of the ovarium in birds are associated with crowing and male plumage, all of which is evidence that the recessive sex asserts itself when the dominant sex becomes impaired, and supports the view held by Heape that there is no such thing as a pure male or female animal. If this be true, it naturally follows that a male ovum is fertilized by a female spermatozoan and a female ovum by a male spermatozoan (Heape). Everything, in fact, points to ova and spermatozoa being sexual—that is to say, there are male and female ova, male and female spermatazoa. Microscopic differences in the structure of spermatozoa have also been observed which have led to their classification into two groups, which are, in all probability, male and female.

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* First practised on the dog by Spallanzani, 1784.

† 'Notes on the Proportion of Sexes in Dogs,' W. Heape, M.A., F.R.S., *Proceedings of the Cambridge Philosophical Society*, vol. xiv., pt. ii., 1907.

The bearing of Heape's work on the determination of sex is of great importance. He maintains that the sex of the offspring is determined at the time of fertilization, and that no influence exerted subsequently can alter it. This is opposed to generally accepted doctrines, but results from an acceptance of his hypothesis that an ovum in which on sex is dominant must be fertilized by a spermatozoan n which the opposite sex is dominant; whether the sex h determined by the ovum or spermatozoan depends upo which is the more powerful of the two.

Heape's study of the ovary of the rabbit* shows tha ova may degenerate, and that one of the chief causes nutrition. It is possible that nutrition has a selecti action on ovarian ova, and so effects a variation in the proportion of the sexes of the ova produced; where no such selective action occurs in the ovary, the proportion of the sexes of ovarian ova produced is governed by the laws of heredity (Heape).

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* 'Ovulation and Degeneration of Ova in the Rabbit,' *Proc. Roy Society*, vol. B., 76, 1905.

Impregnation.—The male element meets with the female in the narrow passage of the Fallopian tube. Bearing in mind the enormous number of spermatozoa in even only a small amount of the secretion, it is easy to understand why the ovum cannot escape coming in contact with them. The ovum is transported towards the uterus by the cilia of the tube, the spermatozoa travel in the opposite direction by means of their own vibratile motion. One spermatozoan suffices for impregnation; it passes through the zona radiata, reaches the vitelline membrane, and when within it the tail is lost, and only the head and part of the middle piece remain. The two pro-nuclei, male and female, come together, and a single nucleus results. The fusion of the nuclear element of these two different cells results in a new structure, the ovum is fertilized, and from this is developed a new being embodying the hereditary properties of both parents.

In the sheep* the impregnated egg enters the uterus on the fourth or fifth day and travels slowly along it until the ninth day. On the ninth day the zona radiata ruptures and the *blastocyst* (that is the external cover of the cellular mass) lies in contact with the uterine epithelium.

On the twelfth day the ovum has reached nearly to the lower limit of the horn in which it lies, the glands of the uterus enlarge, and the blastocyst rapidly elongates so that each end grows out to the tip of each horn of the uterus. If one embryo only be present it extends through both horns of the uterus; if there are two they are each confined to one horn. On the seventeenth and eighteenth day the first attachment of the embryo to the uterus is effected, a very important period in embryonic life. Up to this time the only nourishment available is that furnished by the juices poured into the uterine cavity by the glands, and until the twentieth day the ovum receives no other source of supply but this. On the twenty-eighth day *villi* on the external covering of the embryo are well developed, and on the maternal cotyledons are little depressions into which they fit. The *allantois* (see later) has grown rapidly, and the *yolk sac* (which see) has become reduced as the allantois increases. By the forty-fourth day the fœtal cotyledons are scattered over the whole surface of the embryonic covering. On the seventy-eighth day the general character of the placenta is established. As the uterus swells owing to the increase in size of its contents, it does so generally excepting the upper part of the horns, which are but little longer than normal, and are engaged in active secretion.

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* 'The Morphology of the Ungulate Placenta,' by R. Assheton, M.A., whom in the above account of the sheep we have entirely followed. *Phil. Trans.*, B. vol., 198. 1905.

We have given this condensed account from Assheton of the development of the embryo of the sheep, as we have previously had but little exact knowledge how the embryo of a ruminant comports itself during the early days o development. The development of the embryo of the hors has been dealt with by Ewart,* not with the same degre of fulness as the above, as that is practically impossible but sufficiently so to show not only the characteristi features of the process, but their profound practical bea ing on the hygienic care of brood mares.

We shall see presently that the human decidua grow over the ovum on its arrival in the uterus, and so preven its escape. No such pouch is formed in the ungulate and the escape of the ovum before it is securely fixed to t wall of the uterus is not unlikely, especially in the hor where the connection between the embryonic sac and t uterus is easily broken down. To understand how th occurs Ewart points out that the remote ancestors of t horse were probably born on the forty-seventh or for eighth day of conception, and like the ancient and pri tive mammals the opossum and kangaroo, passed from the uterus to a pouch where they lay securely suspended by a teat until their perfect development was completed. The arrangement by which the equine embryo is anchored, as Ewart calls it, to the wall of the uterus, is in the first instance by some of the cells of the outer layer of the embryo, at a part which is in communication with the yolk sac. This connection (Fig. 144, *a*, *b*, *c*) is of a very slender kind and is the only one which exists up to the fifth week.

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* 'A Critical Period in the Development of the Horse,' by T Ewart, M.D., F.R.S. 1897.

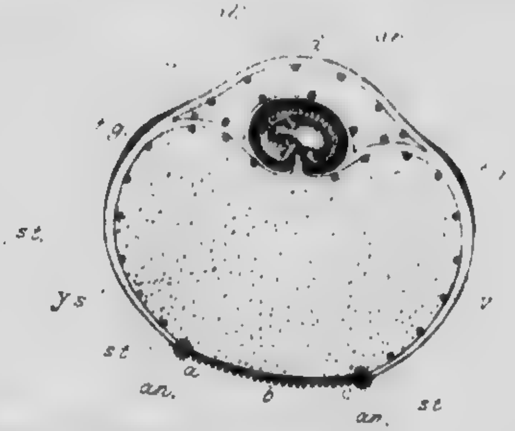

FIG. 144.—SEMI-DIAGRAMMATIC REPRESENTATION OF A FOUR WEEKS HORSE EMBRYO AND ITS FŒTAL APPENDAGES, NATURAL SIZE (EWART).

am., The amnion; *y.s.*, the yolk sac, which is vascular, *v*, as far as the circular bloodvessel, *s.t.*, and crowded with granules which have entered by the absorbing area, *a*, *b*, *c*, of the yolk placenta; *all.*, the allantois. The embryo measures nearly three-eighths of an inch in length, and is curved so that the tail lies under the head.

At the fifth week additional means of securing the embryo to the wall are evident, by an increase in the size and strength of the original yolk sac adhesion. There is also a girdle about ¼ inch wide, not hitherto found in any mammal (Ewart), placed around the equator of the embryo (Fig. 144, *t.g.*). This girdle obtains adhesion to the uterine wall and so strengthens the original anchorage. About the end of the sixth week the attachment of embryo to uterus is again becoming precarious, for the yolk-sac attachment area has become less (Fig. 145, *a-c*), while the girdle has shifted from the equator to near the pole (Fig. 145, *t.g.*). It is at this period Ewart considers the primitive ancestors of the horse were born.

At the end of the seventh week the supply of nourishment through the medium of the yolk sac has nearly come to an end, the absorbing area next the uterus is considerably reduced, and it is at this period when an entirely new source of supply and attachment has to be found. The supply is furnished by means of the *allantois*, while the additional attachment is furnished by the girdle becoming folded into ridges, which fit into grooves and depressions in the mucous membrane of the uterus. The outer cover of the embryo beyond the girdle is now dotted with numerous minute points, which subsequently become villi ; the villi are derived from a sprouting of the allantoic sac, and as they grow are accommodated in pits in the uterine wall. By the end of the eighth week this has been accomplished The villi are not more than ⅛ inch long, even when ful

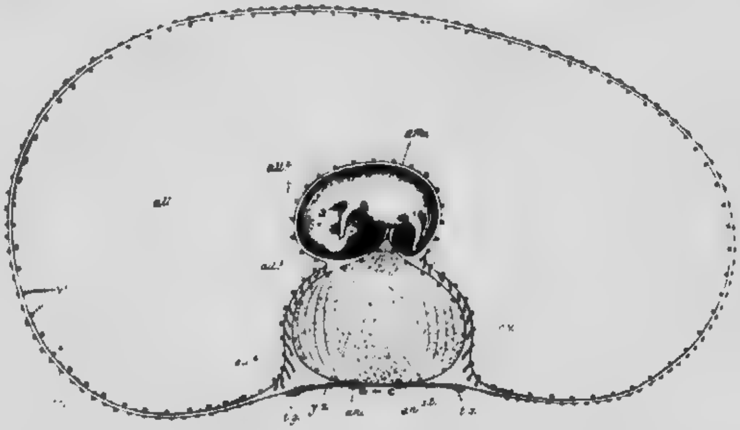

FIG. 145.—A SEVEN WEEKS' HORSE EMBRYO, HALF NATURAL SIZE (EWART).

all., Allantois ; *am.*, amnion ; *c.v.*, non-vascular villi between the allantois and the yolk sac, not hitherto found in any mammal, and function unknown ; *y.s.*, yolk sac ; *a-c*, absorbing area of the yolk placenta ; *v*¹, vascular villi or allantois ; *t.t.*, external vascular villi over the surface of the embryonic sac.

grown, and at birth they are withdrawn from the uterine pits. Once the villi have become established the question of nourishment becomes no longer a difficulty, and the critical stage in the development of the horse is passed.

The cause of mares 'breaking service' from the sixth to the ninth week is answered by Ewart in the light of his inquiries. At the third, sixth, and ninth week the physiological changes associated with œstrus are likely to supervene and shake the reproductive system. At the third week the risk of casting off the embryo is not so great, as the area by which it is attached to the uterine wall is sufficiently large to render it moderately secure, but at the sixth week a change from yolk sac to placental nourishment is being effected, and the yolk sac area is less than it was at the third week. At such a time a contraction of the uterine horn will be followed by expulsion of the embryo. At the ninth week the question of not 'breaking service' depends on whether the villi have appeared in time, and obtained a sufficiently intimate relation with the uterine vessels to supply the embryo with the additional nourishment its development requires, that through the yolk sac being insufficient.

Ewart says that the embryo of the mare usually occupies the right horn of the uterus, and in the early days is suspended by the yolk sac from the upper wall of the organ, the head being towards the body of the womb. Later the fœtus may lie in the body of the uterus, but the hind limbs remain to the last in the right horn.

Development of the Ovum.—Ova are *holoblastic* or *meroblastic* according to the method of segmentation. This depends upon the amount of yolk contained in the egg; if very little or none the segmentation is holoblastic and complete as in the eggs of mammals; if abundant as in birds, the segmentation is meroblastic and partial.

After fusion of the two pronuclei the resulting nucleus begins to divide, and there first results two cells which are not equal in size. These also divide, each into two, and the inequality of size of the first generation is impressed upon the second, and after the third division, when eight cells have resulted, we find four large cells and four somewhat smaller. From this time the smaller cells divide more rapidly than the larger and become superficial, the larger cells remaining in the centre (Fig. 146, I.). Thus as the result of repeated division there results a mulberry mass of cells, the small cells being external, the large cells internal. It is at this stage that the segmenting ovum enters the uterine horn from the Fallopian tube; this has been observed in the rabbit.

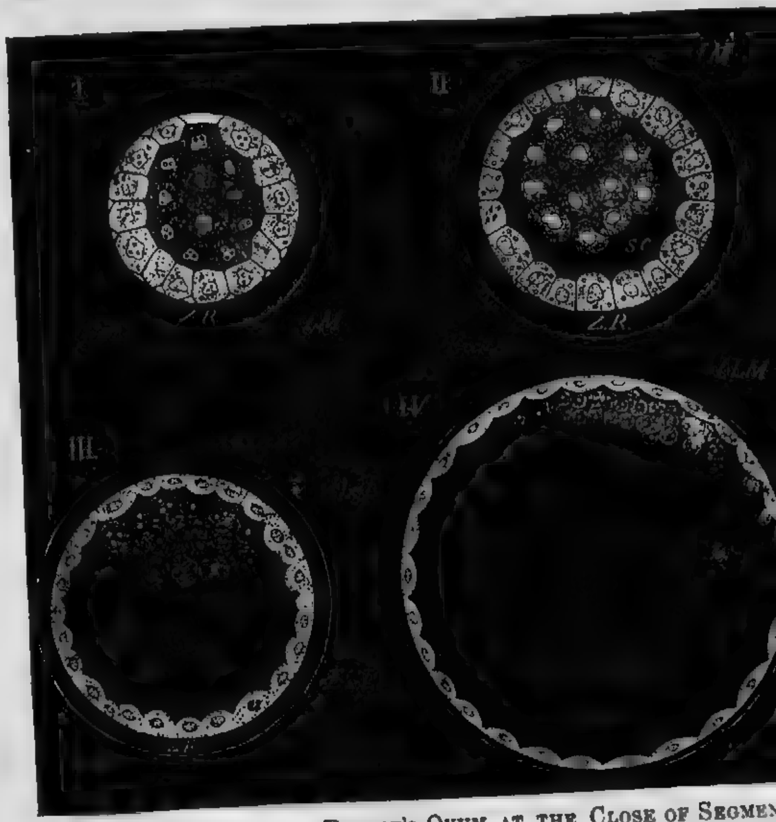

FIG. 146.—SECTION OF A RABBIT'S OVUM AT THE CLOSE OF SEGMEN TION. II., III., IV., STAGES IN THE FORMATION OF BLASTODERMIC VESICLE (E. v. BENEDEN).

Z.R., Zona radiata; *Ex.L.*, External layer of cells; *I.M.*, Inner m of cells; *I.L.M.*, Inner lenticular mass of cells; *s.c.*, Segme tion cavity.

The next change observable is the appearance of the segmente cavity (Fig. 146, II.). This first appears as a cleft between the i large cells and the outer small cells; this rapidly increases in size a expense of the inner cells, which are pressed together forming a like patch within the now hollow sphere of small external cells. is the blastodermic vesicle, and is much larger than the original c

The lens-like mass of inner cells flattens somewhat, still however remaining thicker in the centre; this central thickening being the first sign of the embryonic or embryonal area (Fig. 146, III. and IV.). The spherical blastodermic vesical rapidly becomes ellipsoidal, and the membranes or coverings of the ovum become thin and attenuated; the vitelline membrane indeed may have disappeared.

The next stages in the blastodermic vesicle are not clearly understood, but it appears that the wall of the vesicle is one cell thick except at the embryonal area, where two layers are to be seen. This is the *bilaminar blastoderm*, the superficial layer of which is *epiblast*, the inner *hypoblast*. If the embryonal area be examined from a surface view it is seen to be pyriform in outline, and in its posterior part the *primitive streak* appears. This streak is due to a thickening—to the appearance of the third permanent layer of cells—of the mesoblast, which is derived probably from both epiblast and hypoblast. These three layers constitute the trilaminar blastoderm, from which the various organs and tissues are developed.

From the *epiblast* the following develop: The whole of the nervous system, including the brain, spinal cord, peripheral nerves, and sympathetic system. The epithelial structures of the organs of special sense. The epidermis and its appendages, including hairs, hoofs, and nails. The epithelium of all glands opening upon the surface of the skin, including mammary glands, sweat glands and sebaceous glands. The epithelium of the mouth (except that covering the tongue and posterior part of the mouth which is hypoblastic) and glands opening into it. Epithelial covering of anus. The enamel of the teeth. The epithelium of the nasal passages, upper part of pharynx, and cavities and glands opening into the narial passages, *e.g.*, sinuses of head, etc.

From the *mesoblast:* The urinary and generative organs (except epithelium of urinary bladder and urethra). All the voluntary and involuntary muscles of the body. The whole of the vascular and lymphatic system, including serous membranes and spleen. The skeleton and all connective tissues. The amnion is partly epiblastic and partly mesoblastic.

From the *hypoblast:* The epithelium of the alimentary tract from the back of the mouth to the anus, and all the glands opening into this part of the tract, such as the liver, pancreas, etc. The epithelium of the Eustachian tube and tympanum. The epithelium of the bronchial tubes and air-sacs of the lungs. The epithelium lining the vesicles of the thyroid body. Epithelial nests of the thymus. Epithelium of the urinary bladder and urethra. The allantois is partly hypoblastic and partly mesoblastic.*

At the stage mentioned in a previous paragraph, viz., the appearance of the mesoblast, the hypoblast has grown along the inner surface of the epiblastic layer, and nearly lines the whole blastodermic vesicle, which now becomes ellipsoidal and filled with a coagulable fluid. In front of the primitive streak, the *primitive groove* appears as a linear depression bounded by two ridges, known as the medullary ridges, the groove is the *medullary groove.* The ridges continue to grow upwards, and then to curve inwards and approximate in the middle line from before backwards, forming a tube the foundation of the cerebro-spinal nervous system. If a section of the embryo be taken at this stage across the medullary groove and ridges, we find placed beneath the groove and derived from the hypoblast a mass of cells circular in section, the *notochord* or *chorda dorsalis* (Fig. 147). The notochord, which is rod-like, gives rise to nothing, but around it the vertebral column develops, and rudiments of it are found even in adult life in the pulpy centre of the intervertebral disc. The mesoblast has been rapidly growing as a sheet between the epiblast and hypoblast, and i the young embryo be examined from above, it is seen to be broken u into 'quadrangular masses' the protovertebræ or somites. These somite give rise to portions of the vertebræ and to the muscles of the trunk During the growth of the mesoblast the embryo, which is developin in front of the primitive streak, is being gradually lifted from off th blastodermic vesicle. This is brought about by a process of tucking o folding off, and first appears at the tail-end of the embryo, and extend along either side to the head ; as a result there is a distinct depressio or 'sulcus' surrounding the embryo. The remainder of the blasto dermic vesicle is filled with fluid, and forms the *yolk sac* (Fig. 147), an this may persist in some animals, as the dog, until birth. Man believe that this yolk sac, which in mammalia contains no yolk, but i abundant in birds and reptiles, points to the fact that the ancestors o mammals had large eggs even as the monotremes (prototheria) hav to-day. The eggs of the Ornithorhynchus or duck-mole are as large a a hazel-nut.

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* Schäfer, Quain's 'Anatomy,' vol. i., Part I., p. 44.

The *medullary* or *neural groove*, which has now been converted int a canal, becomes dilated and vesicular in the head region. The vesicles are at first three in number, then five, and give rise to variou parts of the brain. The lumen of the canal and vesicles persists, an we see them in the adult as the minute central canal of the cord, an the ventricles of the brain. The nervous structures of the eyeball a derived as outgrowths of the brain ; the organ of smell is the nasal p innervated from the fore part of the brain ; the ear is an involuti of the epiblast that also speedily receives a nervous supply from t brain. The mesoblast about the time of the formation of the cerebr vesicles splits into two laminæ, and the space between becomes t *cœlom* or body cavity (Fig. 147). The upper lamina, consisting epiblast and mesoblast, is known as the *somatopleure;* the low lamina, consisting of mesoblast and hypoblast, becomes the *splanchnopleure.*

Arising from the somatopleure, at first posteriorly and then at the sides of the embryo, are ridges that grow upwards over the embryo towards the head region, to fuse and form the *amnion* (Fig. 147). In front of the head the mesoblast has not as yet extended, and the epiblast and hypoblast are united forming the pro-amnion. This however soon disappears, and a ridge developed here grows over the head of the embryo to meet those advancing from behind. This fuses with those from the tail and sides, and as a cavity appears in the ridges the embryo has a dorsal covering (Figs. 147 and 148) of two layers, that next the embryo being the true amnion, and this is separated from the outer or false amnion (the chorion) by a cavity into which the allantois grows. Thus the amnion arises from the same portion of the embryo which gives rise to the body wall. The outer membrane of the embryo is an organ of paramount importance, known to morphologists in its early stages as the *trophoblast*, and to the anatomist in its complete

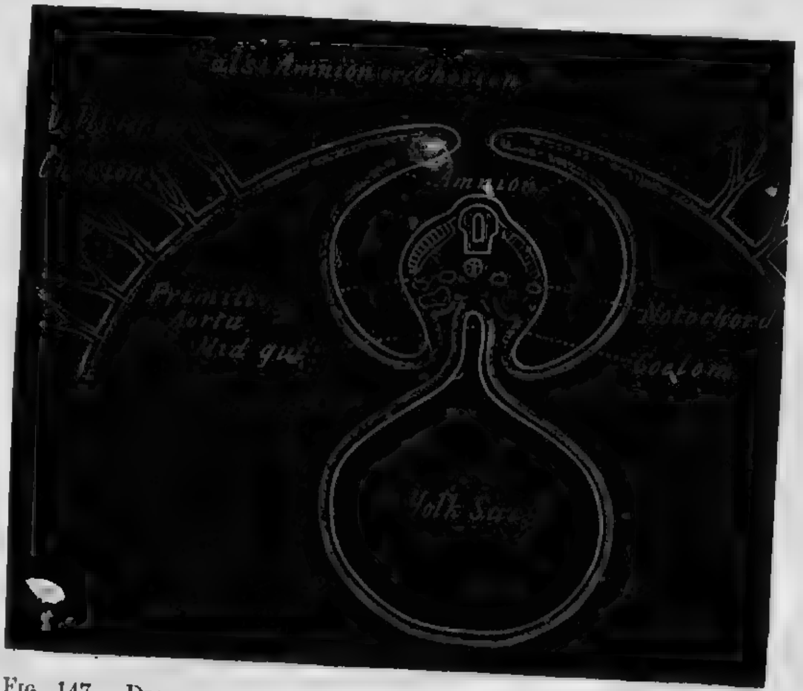

FIG. 147.—DIAGRAM OF A TRANSVERSE SECTION OF A MAMMALIAN EMBRYO, SHOWING THE MODE OF FORMATION OF THE AMNION (SCHÄFER).

The amnion folds have nearly united in the middle line.

form as the *chorion*. It brings about the connection between the fœtus and the mother through the medium of the villi. These villi are received into folds of the uterine mucous membrane, or into uterine crypts, and thus attachment to the mother is secured.

The development of the organs of the body does not enter into a work of this kind; the student, for fuller information, is referred to special works on Embryology. Reference however may be briefly made to the so-called *Chestnuts* and *Ergots* of the horse, both which are ancestral remains, the former being distinctly seen in th fœtus. Both the chestnuts and ergots are considered to be the remai of hoofs, belonging to digits long since lost by the horse. The erg grows from the back of the fetlock. The chestnut is found on the insi of the arms and hocks, and is always larger in the former positio In the heavy type of horse it may grow to a considerable si The horn of which it is composed presents microscopically a tubu

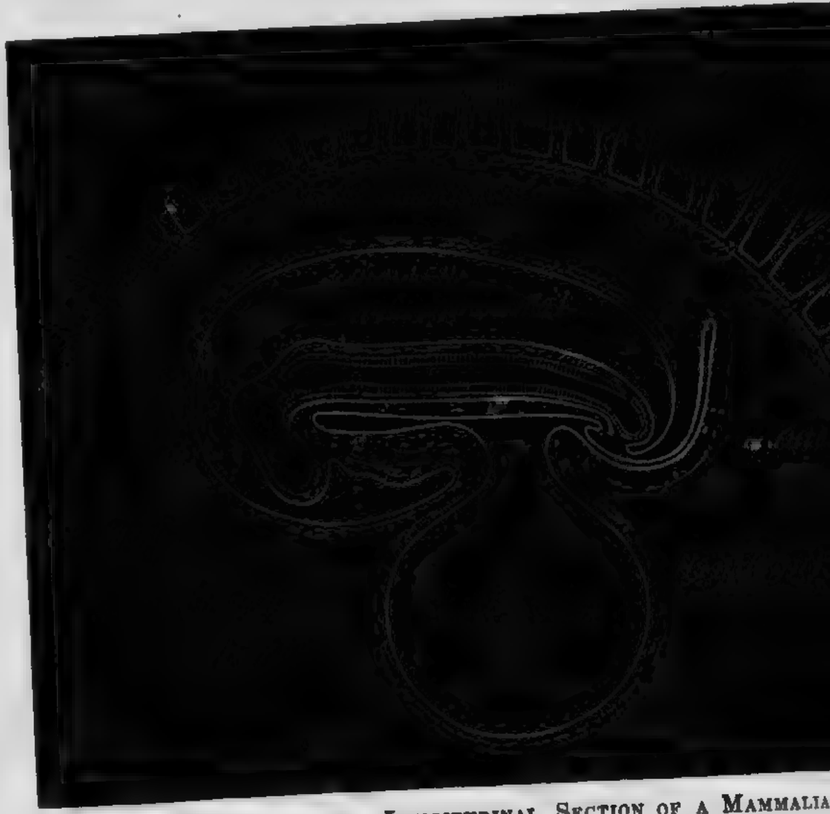

FIG. 148.—DIAGRAM OF A LONGITUDINAL SECTION OF A MAMMALIA OVUM, AFTER THE COMPLETION OF THE AMNION (SCHÄFER).

structure, and is produced by the papillæ of the skin. After growing a certain size it drops or is pulled off. Both ergots and chestnuts are found larger in horses wanting in quality than in those better bred.

The Decidua.—At every monthly period in the human female the mucous lining of the uterus undergoes certain changes which result in the formation of a membrane known as the *decidua ;* this is in shape a counterpart of the interior of the uterus. The membrane is shed during menstruation ; if the woman becomes pregnant the decidua is not exfoliated, but undergoes further development in connection with the ovum. The latter on its arrival in the uterus becomes embedded in the folds of mucous membrane which grow up around and anchor it to the wall of the uterus. That portion of the mucous membrane which grows over and envelops the ovum is known as the *decidua reflexa,* that which lines the interior of the uterus is known as the *decidua vera.* Through the decidua vera the uterine glands grow, and later on in embryonic life when the final circulation is established between the fœtus and the mother, by means of the *placenta,* the latter on the maternal side is attached to a portion of the decidua vera, and to this part the term *decidua serotina* is given. After the birth of the child the membrane covering it, the placenta, and the uterine decidua, are all cast off, with the result that the interior of the uterus is converted into a large raw wound.

Placenta.—No domesticated animal has a decidua ; the ovum is attached in quite another way to the uterine wall, and though a placenta exists it is differently arranged to that of the human female. This has led to the primary classification of placentæ into *deciduate* and *non-deciduate,* but these terms in the light of recent enquiry are not appropriate, for it is no longer a matter of importance from a morphological point of view, whether a portion of the maternal tissue comes away with the afterbirth or not. The most recent work on the placenta of animals suggests another classification.* Assheton proposes to group placentæ into two great types, *placenta cumulata* and *placenta plicata*, these terms being based on the arrangement of a certain group of cells (the *trophoblast*) in the outer layer of the embryo, through which the embryo is secured to the wall of the uterus. Whatever form the placenta may be, or whatever the attachment between the fœtus and the mother, it is always originated by the trophoblast cells.

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* 'On the Morphology of the Ungulate Placenta,' by R. Assheton, M.A. *Phil. Trans.,* B. vol., 198. 1905.

In the cumulate type of placenta the trophoblast cells heap themselves up and *destroy the uterine epithelium*, and form spaces into which the maternal blood escapes, while in the plicate there is no heaping up, but a process of folding and ingrowth takes place, *the uterine epithelium in most cases being left intact.* The pig is the extreme type of plicate placenta, then follows the mare, cow, sheep, while the placenta of man and carnivora is of the cumulate type. It must not be supposed that these types are sharply divided—for instance, the sheep has a plicate placenta which contains cumulate features, and the placenta of the dog though cumulate has features of a plicate type.

Besides recognising placentæ as deciduate and non-deciduate, or plicate and cumulate, they are further classified according to the disposition of the chorionic villi. If the villi are scattered over the whole surface of the chorion the placenta is *diffuse*, as seen in the sow, mare, and camel. The only parts of the chorion in these animals destitute of villi are the poles, and the smooth patch is very minute. If the villi are gathered into tufts upon the surface of the chorion, and these tufts correspond to elevations of the mucous membrane of the uterus, the placenta is *cotyledonary* or *polycotyledonary*. The tufts and elevations are the fœtal and maternal cotyledons respectively, and number sixty more or less. If the villi are disposed in a strap-like manner around the envelopes, leaving the poles for some distance free from villi, the placenta is *zonary*, and such a condition is found in the placenta of the dog and cat. In the rabbit and woman the placenta, from its shape, i discoidal or metadiscoidal.

It is not known how the material passes from the maternal to the fœtal tissues; the blood of the two as previously mentioned does not come in contact, but active changes occur between them through the villi of the placenta. Proteid, fat, carbohydrate, and oxygen are received by the fœtus, and carbon dioxide, nitrogenous waste products, etc., delivered to the mother. The nourishment of the mother directly influences that of the embryo, and pregnant animals imperfectly fed can only produce puny offspring. That material may pass from mother to fœtus is proved by the bones of the embryo being stained if madder be administered to the parent. Yet we know that the placenta, under other circumstances, is an efficient filter for certain pathological substances, and that the tuberculous mother does not convey tuberculosis to the fœtus. It has been suggested that the passage of water, salts, and sugar from mother to fœtus may occur by diffusion, the passage of fat and proteid being perhaps connected with special enzymes. The presence of glycogen in all the embryonic tissues points to it as an important material in the nutrition of the fœtus. Gradually, as development proceeds, the glycogenic function becomes largely centred in the liver and placenta.

Fœtal Membranes.—If the egg of the hen be examined after incubating nine days, the appearance seen in Fig. 149 presents itself. A chick in an advanced stage of development is bound within a thin tough skin, containing fluid; this water-jacket is known as the *amnion*, and its use is to prevent jar when the egg is moved; an identical arrangement exists in mammals. The supply of food required by the embryo chick during development is contained in a sac known as the *yolk sac*, to this food-supply the embryo is connected by a stalk through which the nourishment enters its body. The walls of the yolk sac are vascular and connected with the vessels of the embryo; it is through the medium of the vascular wall that the altered yolk is taken up. A modified yolk sac is found in mammals (Figs. 145, 147, 148); it does not contain yolk, but it takes up the

nourishment secreted by the uterine glands, and for a time this suffices for the needs of the embryo. The chick has another fœtal appendage known as the *allantois*, it grows out from the body, being connected to the embryo by means of a stalk, and forms a vascular sac through which blood from the chick's body circulates. The allantois in the chick is a breathing organ, the air enters through the pores of the shell, and the blood takes up oxygen from the air surrounding the allantoic sac; an air space also exists at the end of the shell. An allantois exists in the mammal (Figs. 145, 148); unlike that of the bird it does not obtain oxygen from the air, though it is a breathing organ in th
sense that it furnishes oxygen to the fœtus.

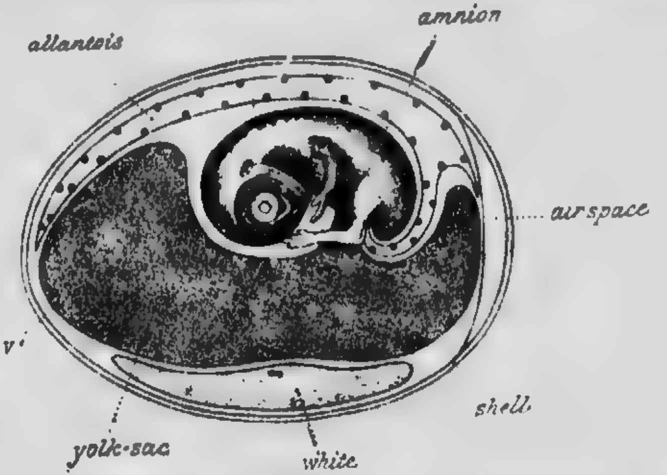

Fig. 149.—Hen's Egg at the Ninth Day of Incubation (Ewar
after Milnes Marshall).

We have seen that immediately enveloping the ma
malian embryo is the *amnion*, Figs. 145 and 148; this s
contains a fluid in which the fœtus lives. The fluid,
liquor amnii, is alkaline in reaction, and yellowish in colo
during the early days of gestation, but reddish towards t
end of it, probably due to discoloration with meconiu
The amniotic fluid contains proteids, mucin, urea, sug
lactic acid, keratin, and some salts; besides these there
also portions of hoof, epithelium, etc., derived from

fœtus. The source of this fluid is probably by transudation from both the fœtus and mother. Indigo blue injected into the vessels of the mother tinges the amniotic fluid, though it does not stain the fœtal tissues.

The function of this fluid is protective to mother and fœtus; the latter lies on it as on a water-bed, and during parturition it assists in dilating the os and lubricating the maternal passage. The *allantois* grows out from the body of the embryo at the future umbilicus; the part within the body forms the bladder, that outside it forms a sac which in the mare completely envelops the amnion (Fig. 150), but in ruminants only partly so (Fig. 151); the bladder and the cavity of the allantois are connected by a canal in the umbilical cord known as the *urachus*. The fluid found

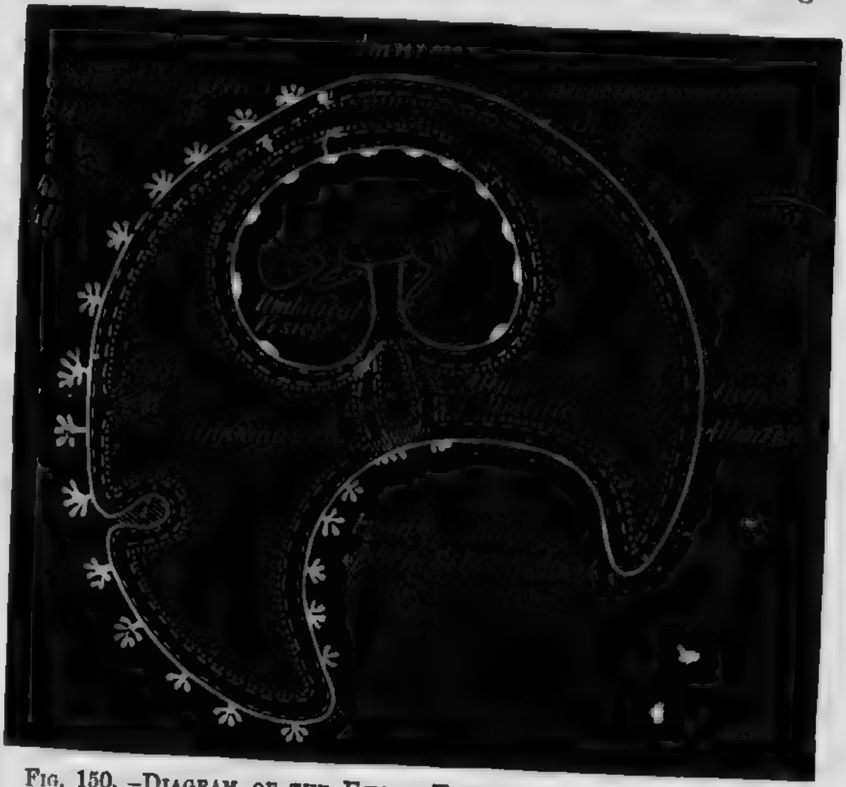

Fig. 150. –Diagram of the Fœtal Envelopes of a Five Months Horse Embryo (Bonnet).

in the allantois is derived from the fœtal urine; in the first instance it is colourless or turbid, later on it becomes brown in tint. This fluid contains urea, and a substance allied to it, allantoin, albumin, sugar, lactic acid, and certain salts. The allantois is the organ of respiration, and to a limited extent of nutrition. During early fœtal life the vascular wall of the allantois is able to bring the blood of the embryo sufficiently near to that of the uterus to effect an exchange of gases. Later on, as we have seen, p. 596, it furnishes the villi which penetrate into the walls of the uterus through the chorion.

Floating in the allantoic fluid of the mare, or attached to the wall of the sac, are certain peculiar masses termed *hippomanes*; their origin and use are quite unknown. It is usually considered that these bodies, which may be multiple, are found in the foal's mouth at birth, but we are assured by a close and reliable observer* that this is a fallacy. Hippomanes have also been observed in the cow.†

The *chorion* envelops the two previous coverings. Through the umbilical cord it forms the vascular connection between the fœtus and the mother, and the villi on its surface project themselves into the mucous membrane of the uterus, not through the medium of a decidua as in the woman, but directly into the uterine wall. The bloodvessels of the chorion and those of the uterus do not anastomose, but the fœtal villi are bathed in the blood contained within sinuses in the uterus into which they run, and in this way, through the endothelial lining of the vessels of mother and embryo, the blood of the fœtus receives oxygen and gets rid of carbonic acid.

Umbilical Cord.—After the formation of the fœtal envelopes the body-walls rapidly close in, the splanchnopleure being received up into the body to form the primitive gut and its

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* Mr. T. B. Goodall, F.R.C.V.S., Christchurch.

† It is a curious fact that even at the present day, in some country districts, hippomanes are sought for in virtue of the properties they have been supposed to possess from time immemorial, viz., for use as love philtres.

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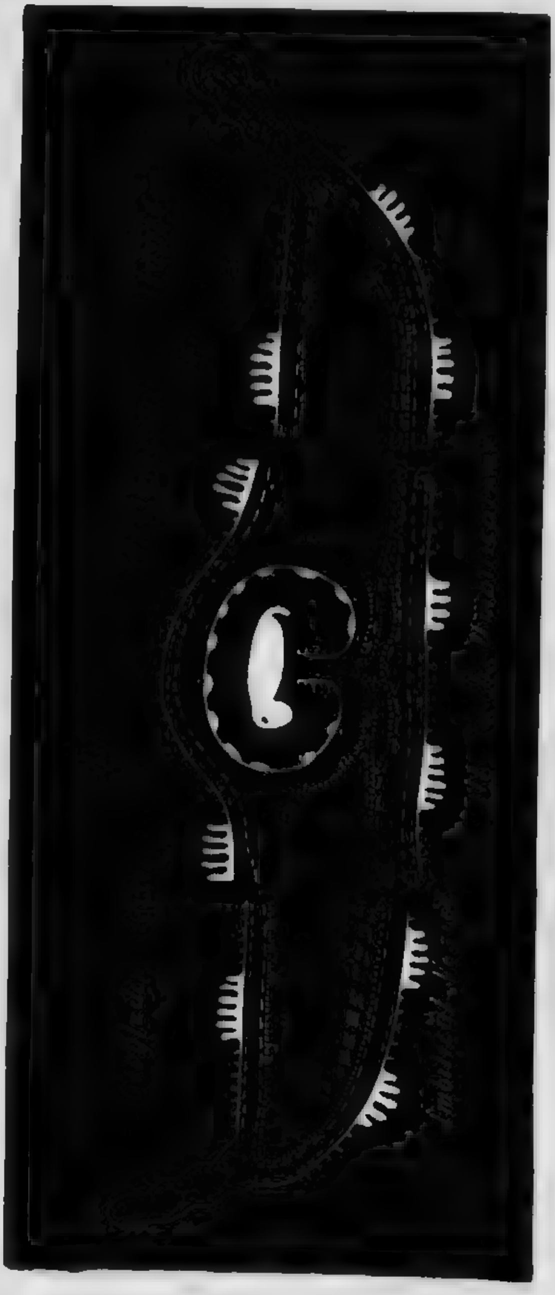

FIG. 151.—DIAGRAM OF THE FOETAL ENVELOPES OF RUMINANTS (BONNET.)
Only the central portion and extremities are represented.

derivatives, the somatopleure forming the body-wall and the limbs. The embryo or fœtus retains its connections with the placenta by means of the umbilical cord, which is composed as follows: Structures in connection with the amnion and the body-wall at the umbilicus; structures in connection with the allantois and the urachus, the latter being a funnel-shaped body connected with the urinary bladder, and the remains of which may be seen as a scar on the fundus of that organ, even in the adult; the umbilical arteries and vein, or veins (ruminants). All these are cemented together by an embryonic connective tissue, the Whartonian jelly.

Fœtal Circulation.—With the formation of the fœtal envelopes and the development of the heart, the circulation takes on a course altogether different from that in the vascular area in early embryonic life. The placenta acts as the fœtal respiratory and food-absorbing organ. Impure blood that has circulated through the tissues of the developing young is brought to the placenta by the umbilical arteries, these acting to the fœtus as the pulmonary arteries to the adult. After an interchange of gases and a renewal of food supply, the blood is carried away to the fœtus by means of the umbilical vein or veins found in the cord. The vein enters the body at the navel or umbilicus, and passes forward along the floor of the abdomen, reaches the falciform ligament of the liver, travels along the free edge of that structure, and empties itself into the portal vein. After birth the remains of the umbilical vein are found as a thickening at the free edge of the falciform ligament, and is named the round ligament of the liver. In ruminants the umbilical veins are two in number, but they unite to form a single vessel on entering the body. The vessel thus formed passes along the abdominal floor towards the falciform ligament to occupy the same position as in other animals, but before reaching it, it detaches a large branch, the *ductus venosus* (Fig. 152, *d v*), which passes upwards to join the posterior vena cava. After the blood has circulated in the liver it leaves by the hepatic trunks, and is poured into the posterior vena cava, where it meets with the blood in that vessel and is thus conducted to the heart. In the horse the whole of the fœtal blood passes through the liver before reaching the heart through the posterior cava; in ruminants part of the blood passes through the liver, and part goes direct to the systemic circulation of the fœtus through the ductus venosus.

In the fœtal heart the cavities of the right and left auricles are in communication by means of a foramen, the *foramen ovale.* This opening in many animals is provided with a valve, the Eustachian valve, that stretches from the mouth of the posterior vena cava to the annulus or thickened border of the foramen ovale; it is absent from the heart of the fœtal horse and pig. The function of this valve is to direct the blood-stream into the left auricle; the blood in this way gets into the left auricle, passes into the left ventricle, and thence into the aorta. The greater portion is driven into the vessels that supply the head, neck, and fore-limbs (anterior aorta and branches), and is conveyed to the head and anterior portion of the body; the remainder passes backwards in the posterior aorta. The head, it will be noticed, receives almost pure blood. After the fluid has circulated in this part of the body, it is returned to the right auricle of the heart by the anterior vena cava. From the right auricle it passes to the right ventricle, and from this cavity it is pumped into the pulmonary artery. The lungs, however, are not functional, and are more or less solid organs, consequently they are not yet prepared to receive the blood as they will be after birth, when they become distended with air and have taken on their duties as breathing organs. The blood must therefore take another course than through the lungs. This course is provided by the *ductus arteriosus* (Fig. 152, *d a*), a short vessel uniting the pulmonary artery to the aorta, and thus bringing their lumina into communication. By this conduit the blood enters the posterior aorta,

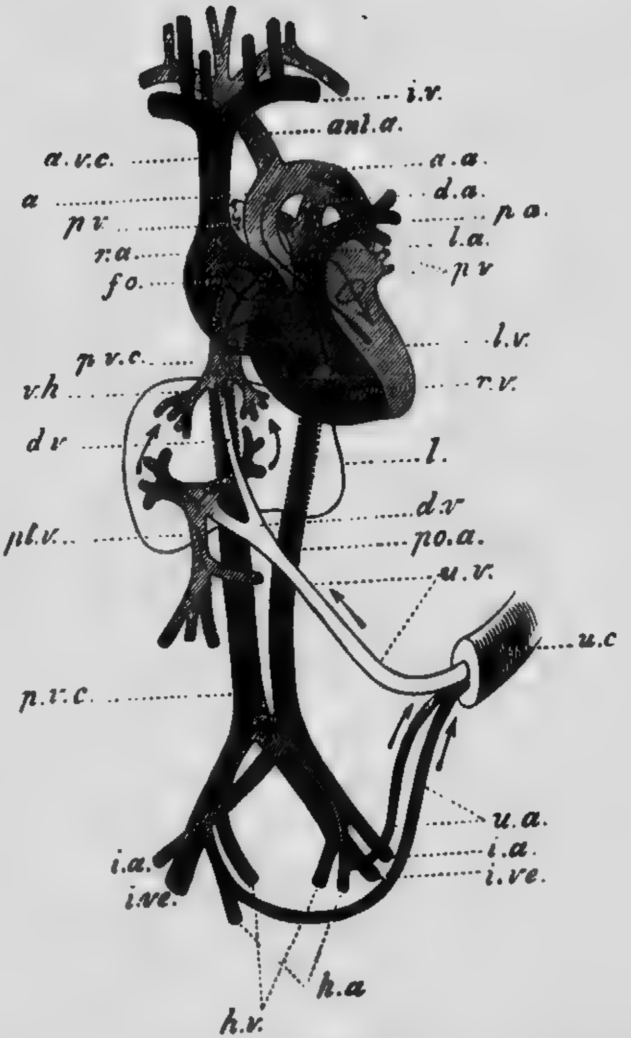

FIG. 152.—DIAGRAM OF THE FŒTAL CIRCULATION (ELLENBERGER)
u. v., Umbilical vein; *d. v.*, ductus venosus; *pt. v.*, portal vein; *l*, live
v. h., hepatic veins; *p. v. c.*, posterior vena cava; *r. a.*, right auric
f. o., foramen ovale; *r. v.*, right ventricle; *p. a.*, pulmonary arter
d. a., ductus arteriosus; *l. a.*, left auricle; *l. v.*, left ventricle; *a.*,
aorta; *a. a.*, arch of aorta; *ant. a.*, anterior aorta; *i.v.*, innomin
veins; *a. v. c.*, anterior vena cava; *po. a.*, posterior aorta; *i.a.*, il
artery; *h. a.*, hypogastric artery; *u. a.*, umbilical arteries; *i.*
iliac veins; *h. v.*, hypogastric veins; *u. c.*, umbilical cord.

The diagram actually represents the fœtal circulation in ruminants; make it applicable to the horse the ductus arteriosus (*d. v.*) m be supposed to be removed, the whole of the blood then traver the liver by the union of the umbilical vein (*u. v.*) with the po vein (*pt. v.*). The arrows indicate the course taken by the blo observe that the stream entering the right auricle divides, passing into the right ventricle, and part into the left au through the foramen ovale (*f.o.*).

and is conveyed to the hinder parts of the body and to the placenta.

The allantoic or umbilical arteries convey the blood from the fœtus to the placenta. These arteries are branches of the internal pudics, or of the parent vessels the internal iliacs, and during intra-uterine life they are larger than the parent vessels. Soon after birth, however, their walls become thickened, and their lumina are lost, and they become impervious to the passage of blood. In the adult they are recognised as the thickened cords found in the lateral ligament of the bladder. The ductus arteriosus just prior to birth has a lumen easily receiving an ordinary cedar pencil, but it steadily diminishes until, at about a month after birth, it is no greater than the diameter of a knitting-needle. It is probable that little blood passes this way after birth, but the exact period of total occlusion is unknown. Similarly the foramen ovale is blocked up by the development of a membrane, which may be pulled out with the forceps shortly after birth, and then resembles in shape an old-fashioned lace nightcap or cowl. When undisturbed it lies in a heap filling up the foramen.

The short cuts in the fœtal circulation, viz., the *ductus venosus, ductus arteriosus*, and *foramen ovale*, exist mainly with the object of ensuring that the purest blood reaches those organs which require it the most. The heart, head, and fore limbs receive blood which is much purer than the blood circulating through the hind limbs and abdominal viscera, for the brain must be well fed. The fact is that the fœtal blood at its best is far below the level of the arterial blood of the mother, and this is explained by saying that the demand of the fœtus for oxygen is small owing to the low rate of its metabolism. From the blood of the umbilical artery and vein of the fœtal sheep the following gases have been extracted, and may be compared with the arterial blood of the mother :

	Umbilical Artery.	*Umbilical Vein.*	*Maternal Arterial Blood.*
Oxygen	2·3	6·3	20·0
Carbon dioxide ...	47·0	40·5	40·0

The liver is a very active organ in the fœtus, and is abundantly supplied with a mixture of blood, the worst and the best in the body, the best predominating. Early in intra-uterine life the liver begins to secrete bile, which is discharged into the intestines as meconium (see p. 212).

Uterine Milk.—If the villi of the chorion be separated from the tubular depressions of the mucous membrane of the uterus, a fluid may be expressed known as uterine milk. This is particularly observable in separating the fœtal and maternal cotyledons. Uterine milk is of a white or rosy-white colour, creamy consistence, and contains proteids, fat, and a small proportion of ash. Examined microscopically it is found to contain globules of fat, leucocytes, rod-like crystals, and structureless masses of proteid. The use of the fluid is for the nourishment of the embryo, and in the mare, cow, and sheep the uterine glands take a prominent part in providing nourishment throughout fœtal life, pouring their secretion into special depressions in the placenta (Assheton).

The **Duration of Pregnancy** appears to be based on no fixed law. Judging from the length of time the elephant is in gestation it might appear that body size had an influence, but against this is the fact that the ass carries her young longer than the horse, while whether it be a toy terrier or a Newfoundland, a dog goes from fifty-nine to sixty-three days. It certainly does appear that among animals of the same species breed has an influence in the matter; different herds of cows vary from 277 to 288 days, Merino sheep average 150 days, Southdowns 144 days. It is not clear why the guinea-pig should require a period of gestation twice as long as the rabbit, which is also a rodent.

The following are average periods of gestation:

Elephant	2 years (nearly).
Mare	11 months, and liable to vary within relatively wide limits.
Ass	358 to 385 days.
Zebra	13 months (and over).
Cow	40 weeks.

Sheep	21 weeks (average).
Camel	45 weeks.
Pig	16 weeks.
Dog	59 to 63 days.
Cat	56 days.
Rabbit	32 days.
Guinea-pig	63 days.

Parturition.—The fœtus having reached its full stage of development, changes of an obscure nature take place which lead to its expulsion. During uterine life the equine fœtus is lying on its back on the floor of the mother's abdomen, with its chin on its chest, the fore-legs bent at the knee, and the hind-legs in the right horn (Fig. 153). Preparatory to birth the fœtus changes position and turns on its side, so as to assume first a lateral position (Fig. 154), and lastly an upright one (Fig. 155), by which the fœtal and maternal spines are brought nearer together. To assume this position the fœtus has had to make a complete revolution; it is now brought with the muzzle and fore-legs in the direction of the pelvis (Fig. 155), and dilatation of the passage follows. In the cow the fœtus lies on its back on the floor of the abdomen as in the mare, but lies somewhat crooked, viz., the head inclining towards one side, and the hind extremities towards the

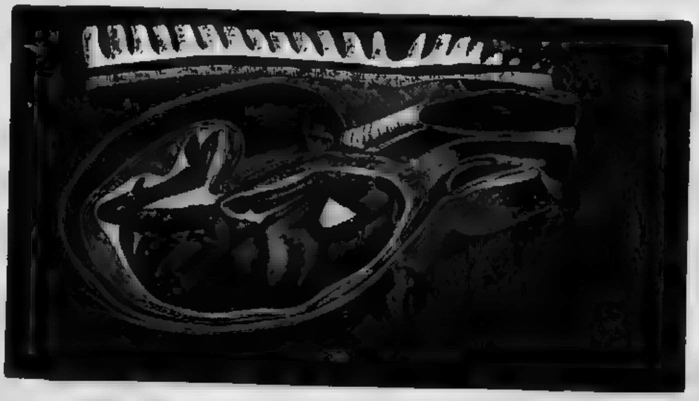

Fig. 153.—The Position occupied by the Equine Fœtus during Intra-Uterine Life (Franck).

other; in all other respects it resembles the mare. The alteration in the position of the fœtus does not occur through its own movements, but by the contraction of the uterus; on the other hand, the stretching of the limbs is the result of fœtal movement.* There can be little doubt that the revolution of the fœtus prior to birth is the explanation of the complete torsion of the neck of the uterus and vagina which is sometimes found in both the cow and mare.

The dilatation of the os is assisted by the amniotic and allantoic fluids. Each contraction of the uterus is accompanied by a pain; the pains last from 15 to 90 seconds, and the interval between them is from 2 to 4 minutes.

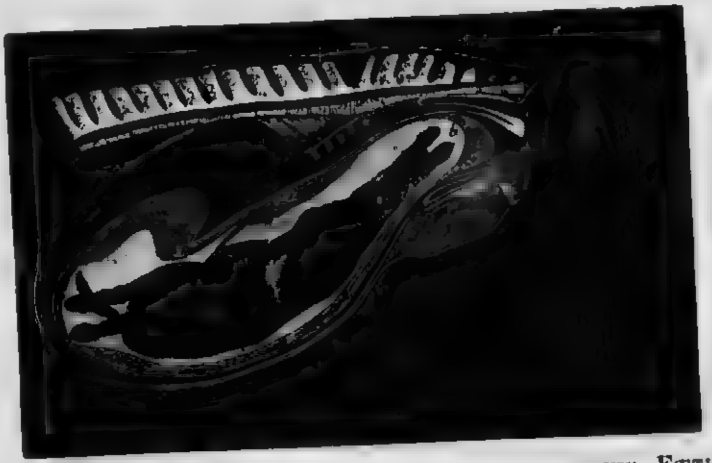

FIG. 154.—THE FIRST STAGE IN THE REVOLUTION OF THE FŒTUS; LATERAL POSITION. THE OS IS DILATED BY THE MEMBRANES WHICH HAVE NOT YET RUPTURED (FRANCK.)

The contractions of the uterus occur under the influence of a centre in the lumbar portion of the cord; they are not under the control of the will, and occur even though the animal be unconscious, or the spinal cord divided in the lower cervical region (dog).

The mare is remarkable for the rapidity with which delivery is effected; ruminants, on the other hand, are often very slow and in labour for hours. Parturition in the mare is accompanied by a complete separation of the chorion from the uterine wall; this is the explanation why any difficulty in foaling invariably sacrifices the life of the foal. In ruminants, on the contrary, the circulation between the mother and fœtus is kept up to the last by the gradual separation of the cotyledons, so that though the process may be delayed several hours, the animal is generally born alive.

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* This description of the change in the position of the fœtus preparatory to birth is taken from Ellenberger's 'Physiologie.'

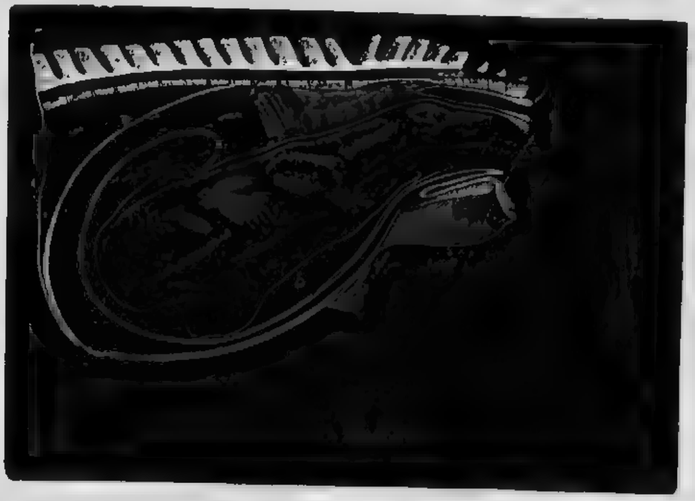


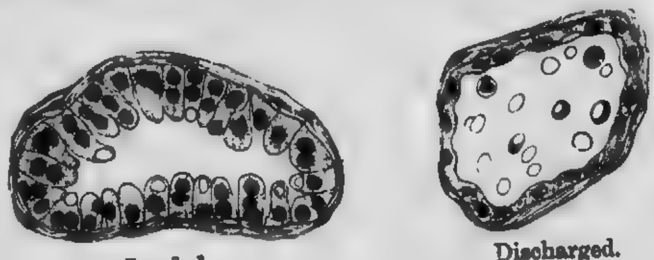
Fig. 155.—The Revolution Completed, Membranes Ruptured, and Foal in the Normal Position for Delivery (Franck).

The cause of the first respiration of the fœtus is dealt with at p. 112.

The Secretion of Milk.

As the period of parturition approaches, the mammary glands become swollen owing to active changes occurring in them, and at or shortly after the birth of the animal milk is formed.

Two processes contribute to the formation of milk; in one the cells lining the alveoli of the gland are bodily shed and form the fat of the milk, while in the other the water, proteids, salts, etc., are formed from the lymph in the gland by the ordinary process of secretion. We mus examine the first of these at somewhat greater length. I the mammary gland of an animal which has never bee pregnant be examined, the alveoli it contains are muc smaller and less numerous than those of a secreting glan The alveoli of the first-mentioned gland are found to b packed with small rounded cells of very slow growth when the animal becomes pregnant the gland enlarge the alveoli increase in number, but remain packed wi cells until parturition approaches or occurs. The sol masses of cells are now cast off, and leave behind the alveoli lined with a single layer of secretory epitheliu



Loaded. Discharged.

FIG. 156.—MAMMARY GLAND OF DOG DURING LACTATION. AF HEIDENHAIN (WALLER).

the function of which is to furnish the milk. The shedd of the mass of cells which originally occupied the alv supplies the colostrum or first milk.

The appearance presented by the single layer of lining the alveolus of the secretory gland, depends u whether the gland is loaded or discharged. If the g is loaded, viz., active secretion occurring, the cells found to be large and columnar in shape, possessing or more nuclei, one being at the base of the cell, the other, giving indications of degeneration, placed the apex (Fig. 156). In the apex or free portions o cell fat globules can be seen, which may even have p extruded themselves from the cell, and besides these are other particles. Further, the cell gives the appea of the apex or free border being separated from the base by a process of constriction.

If the gland be examined when discharged, viz., after the milk has been drawn off, the cells lining the alveolus are cubical or flattened, each containing a nucleus; the lumen of the alveolus is also increased in size, and within it may be seen some of the elements of the milk (Fig. 156).

It is evident that the cells in the active gland are loaded with material, much of it being fat, and these cells break off leaving behind them the parent cell containing a nucleus from which another cell grows. In spite of this the formation of fat in milk is really a process of cell secretion, and this is supported by the fact that animals such as carnivora, whose food is deficient in fat, produce a fat-containing milk, and the fat is elaborated by the mammary cell from the proteid of the body. A fat diet does not increase the fat in milk, though a proteid diet has this effect.

The proteids, sugar, and salts, found in milk are secreted in the ordinary way from the blood, or rather the lymph circulating in the gland, the cells lining the alveolus being the active factor in the matter, and that these substances are really elaborated by the cell, is supported by the fact that neither caseinogen nor milk sugar exists in any other tissue of the body. It has been supposed that the secretion of milk is influenced by the nervous system, but there is no experimental evidence which places this beyond doubt.

Composition.—The milk of herbivora has an alkaline reaction which may readily turn acid; in carnivora the reaction is acid. Fresh cow's milk is *amphoteric*, viz., it gives both an acid and an alkaline reaction to test paper; this is due to the presence of acid and alkaline salts. In the cow the specific gravity is 1028 to 1034. The secretion contains proteids (caseinogen and albumin), sugar (lactose), fats, and salts. An average secretion of milk from a cow may be taken at 6 quarts (6·8 litres) per diem for forty weeks in the year.

In the following table is given an analysis of the milk of different animals:

	Cow.	*Mare.*	*Sheep.*	*Ass.*	*Dog.*
Water	84·28	92·5	82-84	90·5	76·0
Solids	15·72	7·5	15-17	9·5	24·0
Casein	3·57	1·3	4·7	1·7	10·0
Albumin	·75	·3			
Fat	6·47	·6	4-8	1·4	10·0
Lactose	4·84	4·7	3-4·6	6·4	3·5
Salts	·68	·3	·6		·5

It will be observed that the milk of the cow, dog, and sheep is remarkable for the high percentage of fat it contains; the caseinogen of mare's milk is much less than that found in the cow, and more like that of the human. The milk of the dog is rich in caseinogen, fat, and calcium, but poor in lactose.

Under the influence of rennin caseinogen becomes insoluble, and the milk is coagulated, resulting in a *clot* and *whey*; the clot or insoluble casein is now termed *tyrein*. Neither the albumin nor the caseinogen in milk is precipitated by boiling; on the other hand, colostrum is precipitated by heating, and this is due to the fact that it contains globulin. The albumin of milk offers some peculiarities as compared with ordinary serum albumin, and has been termed *lactalbumin*.

The *fats* in milk are olein, stearin, and palmitin, and the proportion of these differs in various animals. The fat is contained within fat globules, and these form in milk a true emulsion, each globule being separated by a layer of milk plasma. On standing the globules rise to the surface of the fluid and form cream; by the process of churning the emulsion is destroyed, and the fat is obtained as butter. Butter consists of 68 per cent. of palmitin and stearin, 30 per cent. of olein, and 2 per cent. of specific butter fats.

Milk sugar or *lactose* is very liable to undergo fermentation, resulting in the production of lactic acid and the curdling of milk. It is not, however, capable of undergoing direct alcoholic fermentation, which would appear to be a provision against fermentative decomposition occurring either in the gland or in the alimentary canal (Lea). The milk of the mare in the presence of suitable ferments may undergo alcoholic fermentation, as in the production of *koumiss*.

The *salts* of milk are principally calcium phosphate, and salts of sodium and potassium. In the composition of the milk we obtain an insight into the nature and quantity of the salts required by growing animals. Bunge gives the following ash analysis of mare's and cow's milk :

	Mare's Milk.	*Cow's Milk.*
Potassium	1·04	1·76
Sodium	·14	1·11
Calcium	1·28	1·59
Magnesium	·12	·21
Iron	·015	·003
Phosphoric acid	1·31	1·97
Chlorine	·81	1·69
Total ash per 1,000 ...	4·17	7·97

The phosphates are increased by those contained in the proteids; they are employed mainly in the construction of the skeleton. The excess of potassium over sodium salts is a feature common to many of the secretions of the herbivora, but in milk, probably in all animals, the ash contains more potassium than sodium. Bunge states that this is due to the fact that as the animal grows it becomes richer in potassium and poorer in sodium salts, depending upon the relative increase in the muscular structure which is rich in potassium, and the relative decrease in the cartilaginous material which is rich in sodium.

Bunge compared the ash of a puppy with the milk of the mother, and the milk with the blood. It was remarkable how closely the composition of the puppy's system agreed with the salts it was receiving in the milk, though when the ash of the milk was compared with the ash of the blood of the mother, the greatest diversity in composition was apparent. In comparing Bunge's analysis of the ash of cow's and mare's milk, one is struck by the fact that the calf requires much more salts for its nutrition than the foal.

The first milk secreted is termed **Colostrum.** The source of colostrum, and some peculiarities in its composition, have already been dealt with. In appearance it is a yellowish white fluid of an alkaline reaction, sweetish taste, and remarkable for the amount of proteid it contains, as much as 15 per cent., whilst ordinary milk only contains 4 per cent. or 5 per cent. Examined microscopically colostrum is found to contain bodies termed 'colostrum corpuscles.' These are large granular corpuscles containing fat.

The use of colostrum is to act as a natural purge, by which means the intestinal canal of the newly born animal is cleared out.

CHAPTER XIX

GROWTH, DECAY, AND DEATH

Growth.—The young of the herbivora very rapidly shake off the helpless condition in which they first find themselves in this world. This is largely due to the fact that they are born with a nervous system in a high state of development; in the course of a few hours they learn to stand and walk, and in a day or two can skip and run. The young animal, moreover, is born in full possession of its senses, such as sight, touch, hearing, smell, taste, and with an amount of intelligence which nearly, if not quite, equals its parents; it practically has nothing to learn but obedience to man. Not only is the nervous system in an advanced condition, but also the locomotor: the legs of the foal are remarkably long, some of the bones being nearly their full length, though, of course, not their full weight; such joints as the knee and hock have very little to grow. We can understand the reason of this development of the limb from what we have previously said, while the length of leg in the foal is undoubtedly for the purpose of enabling the animal to reach the mammary gland.

The limb, however, is only partially developed; from the knee and hock to the ground it is nearly the length of the adult; from the knee to the elbow and the hock to the stifle it is decidedly below the adult; whilst from the elbow to the withers, and the stifle to the croup, the body has a considerable amount to grow. It has been said, and the statement appears to be true, that the future height of the foal may be ascertained by measuring the fore limb from the fetlock to the elbow and multiplying it by two.

TABLE SHOWING THE LENGTH OF THE BONES OF THE LIMBS OF THE FOAL AND ADULT HORSE.

	Adult Horse.	*Foal of Six Weeks.*	*Difference.*
Scapula - - -	15 in.	8¼ in.	6¾ in.
Humerus - - -	12 in.	8 in.	4 in.
Radius and ulna - -	18 in.	12 in.	6 in.
Knee-joint - -	3½ × 3½ in.	3 × 3 in.	½ in.
Metacarpal - -	9½ in.	8¾ in.	¾ in.
Suffraginis - -	3¼ in.	3 in.	¼ in.
Femur - - -	17 in.	10½ in.	6½ in.
Tibia - - -	13½ in.	9½ in.	4 in.
Calcis to metatarsal bone	6 in.	5 in.	1 in.
Metatarsal - -	11 in.	10 in.	1 in.
Suffraginis - -	3½ in.	3 in.	½ in.

The hind quarters of the foal are in a more advanced state of development than the fore; the shoulders are very oblique, the chest contracted and shrunken-looking, and neither contains much muscle. The oblique position of the scapula is due to the weight of the body on the limbs, the weakness of the muscles at this part allowing the angle formed by the scapula and humerus to be considerably closed, and the shoulder-joint to bulge. The head of the foal is prominent over the brain and depressed over the nasal bones. The hair is fully developed but woolly, that of the mane being scanty, and of the tail curly, while the colour of the body-hair is light of its kind. A similar deficiency of pigment is observed in the iris.

The rate at which the foal increases in weight, and other circumstances connected with its nutrition, were made the subject of inquiry by Boussingault.* He found that the mean weight at birth was 112 lbs., that during the first three months the daily increase in weight was 2·2 lbs.: from three up to six months the increase was 1·3 lbs., and from six months up to three years of age the increase was at the rate of ·7 lb. per diem.

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* Quoted by Colin.

The influence of feeding on development is most remarkable; not only does the body increase in size and weight, but the animal presents the appearance of the adult, so that a thoroughbred at two years old is 'furnished' and looks as old as an ordinary horse at four years old.

Calves, according to Torcy,* have a mean weight at birth of 77 lbs., the daily increase during the first two years being 1·5 lbs. With sheep the daily increase in weight is more rapid; a lamb will in ten days gain 50 per cent. on its original weight, will double its weight at the end of the first month, and treble it at the end of the second. Swine present, however, the most rapid increase in weight, for, according to the authorities quoted, a pig will increase 20 per cent. in its weight per diem during the first week, and up to the end of the first year will add ·44 lb. daily to its body weight.

The relative rate of growth of each part is not the same. The eyes, ears, brain, kidneys, and liver grow less rapidly than the other parts, owing to their relatively large size at birth; the greatest increase is in the skeleton and muscles, and to the rate of this increase we have just alluded; the least increase is in the eyes and the ears, and the limbs below the knee and hock. Few observations have been made on the rate of growth. Percival† many years ago drew up a table, which he considered very imperfect, as to the rate at which some horses of his regiment grew, from which he showed that the increase in height between 2 years and 3 years was on an average one inch, between 3 years and 4 years one-third of an inch, and between 4 years and 5 years one-third of an inch. Some of the horses did not grow:

> Of 35 two-year-olds, 2 did not grow during the year.
> Of 144 three-year-olds, 17 did not grow during the year.
> Of 48 four-year-olds, 7 did not grow during the year.
> Of 11 five-year-olds, 2 did not grow during the year.

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* Quoted by Colin.

† 'Lectures on Form and Action.'

There can be no doubt that many horses grow much more than two-thirds of an inch between three and five years old. It is probable that many grow up to their sixth year.

During the time the calf and foal are receiving their mother's milk the urine is acid, for the reason that the animal is practically carnivorous; once a vegetable diet is taken the urine becomes alkaline, and it is probable decreases in quantity. The activity of certain glands, such as the thymus, becomes considerably reduced as the animal grows, and finally they disappear at the adult period. One characteristic of the young animal is the necessity for sleep; it is probably during slumber that the tissues make the immense strides noticeable during the first few weeks of life.

Dentition commences immediately at birth, if it has not already commenced *in utero;* the following tables show the period at which changes take place in the teeth from birth to adult age:

HORSE.

	Eruption.	*Change.*
Incisors:		
Central	At birth.	2½ years.
Lateral	1 to 2 months.	8½ years.
Corner	7 to 8 months.	4½ years.
Molars:		
First	At birth.	2½ years.
Second	At birth.	3 years.
Third	At birth.	About 8½ years.
Fourth	About 1 year.	
Fifth	About 2½ years.	
Sixth	About 3½ to 4 years.	
Canines	About 4½ years.	

Ox.*

	Eruption.	Change.
Incisors :		
Central - -	At or soon after birth.	$1\frac{9}{12}$ years.
Middle - -		$2\frac{2}{12}$ to $2\frac{6}{12}$ years.†
Lateral - -		$2\frac{8}{12}$ to 3 years.†
Corner - -		$2\frac{9}{12}$ to $3\frac{6}{12}$ years.†
Molars :		
First - -	At birth.	About $2\frac{3}{12}$ years.
Second - -		About $2\frac{3}{12}$ years.
Third - -		About $2\frac{6}{12}$ years.
Fourth - -	6 months.	
Fifth - -	About 12 months.	
Sixth - -	21 months.	

SHEEP.

	Eruption.	Change.
Incisors :		
Central - -	At birth or soon after.	About 1 year.
Middle - -		About 2 years.
Lateral - -		Soon after 2 years.‡
Corner - -		About 3 years.‡
Molars :		
First - -	At birth or soon after.	Soon after 18 months.
Second - -		About 2 years.
Third - -		
Fourth - -	3 months.	
Fifth - -	9 months.	
Sixth - -	18 months.	

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* The age of the ox, sheep, and pig is tabulated from the data given by Professor Brown in his 'Dentition as Indicative of the Age of Animals.'

† There is considerable variation in the development of these teeth.

‡ These teeth are liable to great variation in their development.

PIG.

	Eruption.	*Change.*
Incisors :		
Central	1 month.	12 months.
Lateral	2 months.	18 months.
Corner	At birth.	8 months.
Molars :		
First	1 month.	About 15 months.
Second		
Third		
Fourth	5 months.	
Fifth	10 to 12 months.	
Sixth	18 months.	
Premolars	5 months.	
Tusks	At birth.	9 months.

In all these tables the periods given are those of eruption only; the teeth are not fully developed for some time later, which varies from four to six months in the horse to a month in the pig and ruminant.

The completion of dentition marks the age of maturity; the uncastrated animal presents very distinctive features as compared with the female, viz., greater bulk, a heavy crest and neck, and a harsher voice; the castrated horse more closely resembles the mare. No such difference as is observable in the human family exists between the male and female of the horse tribe; the mare arrives at maturity at the same time as the horse, and the castrated animal is not deficient in stamina, strength, or capacity for work; moreover, castration in the horse does not lead to a deposition of fat in the body.

Decay.—It is doubtful to what age a horse would live if not subjected to domestication, but we may safely say that at seventeen years old the powers of life in the majority of them are on the wane, though at this period some may be found in full possession of life and vigour. These are probably cases of a survival of the fittest, and cannot be taken as a general guide. As a broad rule it may be stated that an old horse is liable to be killed by a hard day's work, and in this sense he is certainly old at seventeen. Arterial degeneration is not marked at this period of life, and few horses live long enough for their arteries to become rigid.

Doubtless the work performed by horses is the chief cause of their rapid decay, for their legs always wear out before their bodies; but apart from this, changes in their teeth, such as the wearing away of the molars, appear to preclude many of them from reaching a ripe old age, though instances are on record of horses attaining the age of thirty-five, forty-five, fifty, and one animal is known to have lived to sixty-two years of age. Blaine* appears to have gone very carefully into the question of old age in equines, and he drew the following comparison, which is doubtless very close to the truth:

'The first five years of a horse may be considered as equivalent to the first twenty years of a man; thus, a horse of five years may be *comparatively* considered as old as a man of twenty; a horse of ten years as a man of forty; a horse of fifteen as a man of fifty; a horse of twenty as a man of sixty; of twenty-five as a man of seventy; of thirty as a man of eighty; and of thirty-five as a man of ninety.'

Death.—Death from natural causes in the horse is a matter of rare occurrence; it is seldom that an animal is taken such care of that the tissues are worn out by age and decay, or that he is allowed to live until the breath of life passes gradually from the body. Sentiment plays no part in horse management; a useless mouth is one to be got rid of. In consequence, the majority of horses meet either with a violent death or one the result of disease.

Natural death is described as commencing either at the heart, lungs, brain, or blood. Probably in the main most cases of natural death may be attributed to a failure of the heart's action; but from what we know of the physiology of the heart, respiration, and blood, it is very difficult to separate these in discussing the causes of natural death, knowing as we do how completely one is dependent on the other. The cessation of the heart's action may be looked upon as the termination of life.

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* 'Encyclopædia of Rural Sports.'

We cannot enter upon the cause of death the result o disease, excepting to notice the interesting fact that horses seldom die quietly; a large majority of them leave thi world in powerful convulsions, fighting or struggling t the last, lying on their side, and galloping themselves t death. Especially is this marked in acute abdomina trouble. The struggles at the end should not be mistal for pain; the animal is quite unconscious. The viol convulsions which occur at the last moment are not pres in death from acute chest diseases; such cases stand p sistently to the last, and either drop dead or die v shortly afterwards.

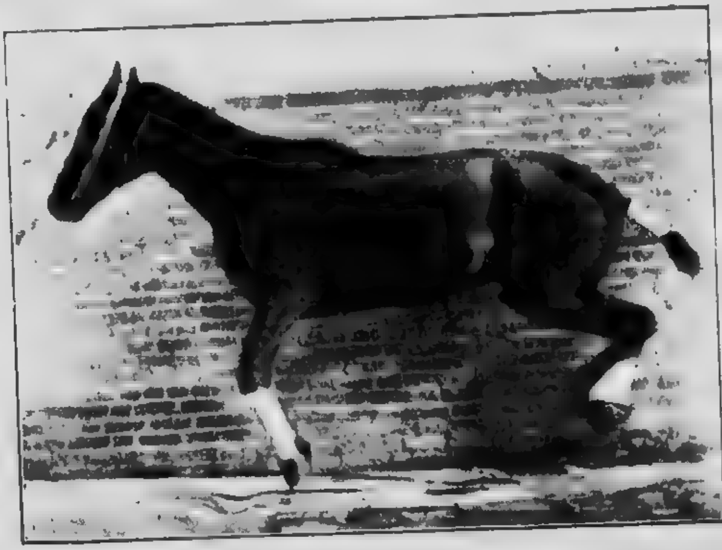

FIG. 157.—CONVULSIVE LIMB MOVEMENTS AT THE MOMENT OF BRAIN DESTRUCTION.

Note the tail is affected as well as the limbs. The bandages are on to assist the plate.

In violent death by destruction of the brain in hor remarkable muscular contractions of the limbs occ these cannot be seen with the unaided eye as they are rapid, but are readily revealed by the camera (Fig. 1

In spite of their rapidity, a marked interval between brain destruction and muscular contractions occurs; in Fig. 158 the brain was destroyed by a charge of large shot, yet the horse is still standing, the impulses relaxing muscle tonus not yet having had time to pass out. At the moment of death the bladder and rectum are emptied, the horse sweats on the inside of the thighs, the pupil dilates widely, and occasionally the *panniculus* is called into play and the animal may shake the skin as if to dislodge a fly.

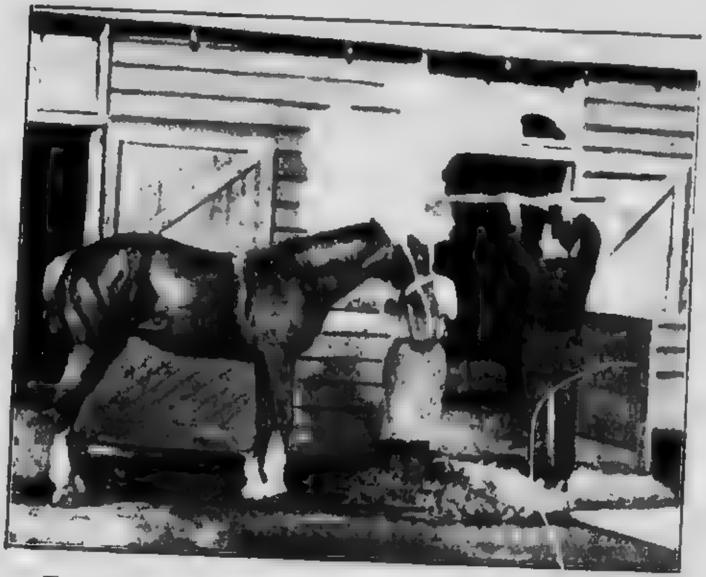

FIG. 158.—BRAIN DESTROYED BY A CHARGE OF SHOT.

The muscles of the quarters are preparing to contract, as may be seen by their outline; the tail is also turned to one side, and the heel of one limb has left the ground. There is nothing, however, to indicate the fact that the horse is dead.

Soon after death *rigor mortis* appears (see p. 379), and within a short time tympany of the abdomen is apparent in the herbivora, reaching such a degree in a few hours, especially during warm weather, that post-mortem ruptures of the diaphragm and other viscera are exceedingly common. The explanation of the tympany is the considerable amount of gas generated by the fermentative decomposition of vegetable food.

CHAPTER XX

THE CHEMICAL CONSTITUENTS OF THE BODY*

A LARGE number of elements enter into the composition of the body. Oxygen, hydrogen, carbon, nitrogen, sulphur, phosphorus, chlorine, fluorine, silicon, potassium, sodium, calcium, magnesium, and iron are found, not, it is true, in a free state or only to a very slight extent, but brought together in such a way as to form compounds, and these may be divided into two classes, organic and inorganic.

Carbon is present in the atmosphere in small amounts in the form of carbonic acid, viz., united to oxygen; it is only in this form that it can be taken up by plants, which in their special laboratory split off the oxygen molecule and store up the carbon, returning the oxygen to the air, and thus supply to the atmosphere that element of which animals are continually depriving it.

Carbon enters the animal system with the carbon of the food, and leaves it either as carbonic acid or in compounds, such as urea; as carbonic acid, therefore, it is again taken up by the plant.

Hydrogen does not occur in a free state in nature, but principally as water, and a very small quantity as ammonia, and it is in these forms that hydrogen is taken up by plants. Animals give off hydrogen as water and ammonia, or as substances which may be readily made to yield these.

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* This brief outline of the chemistry of the body was originally based on a summary of the principal facts contained in Bunge's 'Physiological and Pathological Chemistry,' and Sheridan Lea's appendix to Foster's 'Physiology,' 'The Chemical Basis of the Animal Body.' This chapter is in no way intended to be a complete statement as to the chemical constituents of the animal body, but elucidatory and supplementary to the chemical statements scattered throughout the preceding chapters.

Oxygen is the most widely distributed of the elements, forming one-quarter by weight of the atmosphere, and eight-ninths by weight of water; it also forms, by means of its compounds, one-half the weight of the earth's crust. It is the only element which enters the animal or vegetable body in a free state.

Nitrogen exists largely in a free state, since it forms no less than four-fifths of the atmosphere; it has but little affinity for other elements. In the form of ammonia, nitrous and nitric acids, it enters the plant; as proteid it enters the animal, leaving it as urea, etc., which by decomposition readily yields ammonia. The animal cannot utilize free nitrogen any more than the plant can, though leguminous plants appear to utilize the atmospheric nitrogen by symbiotic co-operation with certain bacteria. As a gas it is found dissolved to a slight extent in some of the fluids of the body.

Sulphur exists largely in nature in combination as sulphates of alkalis and alkaline earths; in this form it is taken up by plants, and becoming a part of their proteid molecule is taken into the body of the animal, where by splitting up and oxidation it yields sulphuric acid, in which form it is excreted in the urine as sulphates or colligated with certain organic substances (see p. 300).

Phosphorus enters plants as phosphoric acid united with alkalis; in soils it exists in only small quantities, hence the necessity of phosphates as manure. In the plant phosphoric acid forms a part of the complicated compounds known as lecithin and nuclein, in which condition it enters the animal body, forming a part of both the solid and fluid tissues.

Chlorine does not exist in a free state in nature, but combined with potassium and sodium, in which form it enters plants, and from these passes in the same compounds into animals.

Neither sodium, potassium, nor magnesium enter or leav
the body or plant in any organic form, but simply as in
organic salts. On the other hand, Bunge considers tha
calcium does enter the body as an organic compound.

Iron does not occur free in nature, but chiefly as com
pounds with oxygen in a ferrous and ferric state. In th
animal it occurs chiefly in the highly complex body hæmo
globin, which acts as an oxygen-carrier. Iron furnishe
the plant with its colouring matter, for chlorophyll cann
be formed without its aid. It is not known in what for
iron leaves the body.

Silicon, in the form of silicic acid, is taken up by plant
From the plant it is taken into the body and passes int
the tissues. It is largely of use in the growth of hair, an
much of it passes out of the body of herbivora with th
urine; in sheep, according to Bunge, it sometimes caus
stone in the bladder.

Bunge draws a contrast, in the following terms, betwe
the methods employed by the vegetable and animal organis
in the utilization of the various elements and compoun
presented to them:

1. The plant forms organic substances; the anim
destroys organic substances. The vital process in the pla
is preponderatingly synthetic, in the animal analytic.

2. The life of the plant is a process of reduction; the li
of the animal a process of oxidation.

3. The plant uses up kinetic energy and produc
potential energy; the animal uses up potential energy a
produces kinetic energy.

The organic compounds in the body may be broa
divided into nitrogenous and non-nitrogenous.

NITROGENOUS BODIES.

Proteids.—This term is applied to a large number
substances more or less closely allied, which in one fo
or other go to make up by far the largest portion of t
animal body.

Proteids are highly complex substances, possessing as yet no definite chemical formula owing to the difficulty in obtaining them in a sufficiently pure state for analysis, and to the magnitude of their molecule. With some few exceptions they have never been obtained in a crystalline condition, and their nature is colloidal, for they do not diffuse through an animal membrane, not even those which can be obtained in a crystalline form.

All proteids contain carbon, hydrogen, oxygen, nitrogen, and very variable amounts of sulphur.

Carbon	51·5 to 54·5	per cent.
Hydrogen	6·9 to 7·5	"
Oxygen	20·9 to 28·5	"
Nitrogen	15·2 to 17·0	"
Sulphur	0·8 to 2·0	"

In spite of the fact that proteids exist in several forms in all animal and vegetable bodies, and that it is quite impossible to maintain life without them, yet very little is known of them owing to their extreme complexity. Neither their chemical formula nor their molecular weight is known, though the latter must certainly be very large, and the chemist has never as yet been able to build them up synthetically, though the work now being carried on by Emil Fischer and his pupils is full of promise for a future synthesis.

The decomposition products of proteids are very numerous and very varying in nature, according to the methods employed. In the body carbonic acid, water, urea, and uric acid are the final end products, but between these and proteids are glycine, leucine, and other substances. From the non-nitrogenous portions of the proteid glycogen and fat may be obtained, as we have previously seen. Proteids, when acted upon outside the body by means of heat, putrefaction, acids, alkalis, and oxidizing agents, yield a large and numerous class of substances.

In the absence of adequate chemical knowledge, all classification of proteids must necessarily be artificial, and

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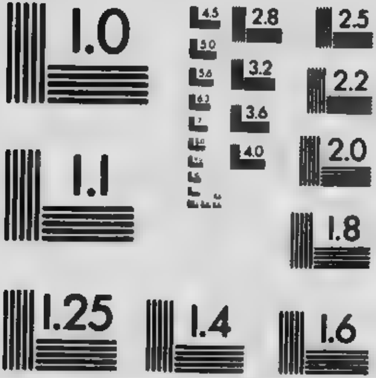

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is at present based on their varying solubilities in water,
saline solutions, acids, and alkalis.

In the following table the proteids are thus roughly
classified, and the distinguishing characteristics of each
class given.

Classification of the Proteids.

A. SIMPLE PROTEIDS.

CLASS I. *Native Albumins.*

These are soluble in distilled water, and the solution
are coagulated by heat at 70° to 75° C., especially in th
presence of dilute acetic acid. They are not precipitate
by saturating their solutions with neutral salts other tha
sodio-magnesium sulphate and neutral ammonium sulphat
Examples of this class are egg and serum albumin, cel
muscle, and milk albumin, or lactalbumin (p. 620).

CLASS II. *Globulins.*

These are insoluble in distilled water, but soluble i
dilute saline solutions ; from these they are precipitated b
saturation with common salt or magnesium sulphate. I
this class are found the globulin of the crystalline le
(crystallin), the globulin of the blood, para- or serun
globulin, the fibrinogen of the blood- and myosin of muscl

CLASS III. *Derived Albumins (Albuminates).*

These are obtained by the action of acids or alka
on albumins or globulins. They are insoluble in distill
water or in dilute neutral saline solutions, but soluble
acids and alkalies, and the solution is not coagulated
boiling, though it is precipitated by careful neutralizatio
Examples of this class are acid albumin, syntonin, a
alkali albumin. Caseinogen (casein), which was at one ti
placed in this class, is now known to be a nucleo-proteid

CLASS IV. *Fibrins.*

These are insoluble in water, but soluble by the p
longed action of strong neutral saline solutions, where

they are largely changed into globulins (Class II.), and with difficulty in strong acids and alkalis, being at the same time converted into acid or alkali albumin (Class III.). Examples are the fibrin formed during the clotting of the blood and lymph.

Class V. *Coagulated Proteids.*

Any of the above which have been coagulated either by heat or the prolonged action of alcohol.

Class VI. *Albumoses* (*Proteoses*) *and Peptones.*

Both of these are very soluble in water, albumose being precipitated by saturation with ammonium sulphate, while peptones are not. Peptones are not precipitated by any ordinary proteid precipitant excepting alcohol, and even the prolonged action of alcohol does not coagulate them. Albumoses may be precipitated by the careful addition of nitric acid in the cold, and the precipitate characteristically disappears on heating and reappears on cooling.

Albumoses (or proteoses) are formed as the *primary* product of the action of the gastric and pancreatic enzymes on proteids. Three well-marked forms of albumose are known, characterized by their varying solubilities and their precipitability by neutral salts or acetic acid and potasssium ferrocyanide. Peptones are the *final* product of the action of gastric and pancreatic enzymes on proteids. One of their most interesting characteristics is that they, alone among proteids, are diffusible through membranes. They differ from albumoses by the fact that they are not precipitated when their solution is saturated with neutral ammonium sulphate or any other neutral salt.

B. Compound Proteids.

Class I. *Nucleo-proteids.*

The nucleo-proteids are, as the name implies, compounds of a proteid with nuclein, the characteristic constituent of nuclei. They form the bulk of the proteids present in most cell protoplasm and their solubilities are closel similar to those of the globulins. Their compound natur is shown by the fact that when digested with gastric juic they yield albumoses and peptones, together with an undissolved residue of nuclein. Ordinarily the nuclein thu obtained is the true nuclein, which yields substances of th xanthine (purin) series when hydrolyzed by acids. I other cases the nuclein residue (pseudo-nuclein) does no yield xanthine bodies by hydrolysis, and typical example of this form of nucleo-proteid are found in the caseinoge (casein) of milk and the vitellin of egg-yolk. They a contain phosphorus, since this element is characteristicall a constituent of nuclein.

CLASS II. *Glyco-proteids.*

These forms of proteid are characterized by yielding, c hydrolysis, some kind of (carbohydrate) substance whic reduces Fehling's fluid and gives osazones with pheny hydrazine. This reducing substance frequently contai nitrogen, and is probably in many cases glucosami ($C_6H_{11}O_5.NH_2$), or amido-glucose.

The characteristic members of the glyco-proteid grou are the various kinds of mucin. Of these the mucin saliva may be regarded as the truest and most typic form. Mucin confers on its solutions their well-know viscidity or 'ropiness.' From these it is readily preci table by the addition of acetic acid, and is resoluble alkalis.

The Albuminoids.

Under this name a number of substances are group together, which, while closely allied to the proteids, dif from them in some important particulars, and differ al in many respects the one from the other. The best know members of the group are collagen and gelatin, chondr elastin, and keratin.

Collagen is the ground substance of which the fibres connective tissue are formed and, under the name of osse forms a large part of the organic basis of bones. It is insoluble in water, salt solutions, and dilute alkalis and acids, though it swells up as a gelatinous mass by the action of the latter. Prolonged boiling with water, especially in presence of dilute acids, converts it into gelatin, and the latter can be reconverted into collagen by a dry heat of 130° C.

Gelatin.—A common and well-known substance of which isinglass is a typically pure form and glue an impure. Insoluble in cold water, it swells up by its action, and now dissolves readily when heated, the solution forming a jelly on cooling, even when it contains only 1 per cent. of gelation. When digested with pepsin or trypsin, gelatin yields *diffusible* substances known as gelatin-peptones. By hydrolysis it yields leucine and glycine, but no tyrosine or any member of the aromatic series, and hence gives no red reaction with Millon's reagent (see below).

Chondrin.—This is obtained from hyaline cartilage by those processes which, when applied to connective tissue or bones, yield gelatin. Chondrin resembles gelatin in that its solutions gelatinize on cooling, but it differs chemically in many respects from gelatin. Thus it is precipitable by acetic acid, and when hydrolyzed yields a substance which reduces Fehling's fluid.

Elastin.—This is the ground substance of the fibres of elastic tissue. It is extraordinarily insoluble and resistant to ordinary reagents, and is hence obtained by treating a tissue such as ligamentum nuchæ with a succession of reagents which dissolve out everything except the elastin. By digestion with pepsin or trypsin or by hydrolysis, elastin yields products similar to many of those similarly obtainable from true proteids.

Keratin.—The characteristic constituent of epidermal structures such as hair, nails, feathers, and horn. From these it is obtained as a residue by their extraction with a series of reagents, such as water, alcohol, ether, dilute acids, etc. Its elementary composition is closely allied to that of the true proteids, but it differs from them by the large amount of loosely combined sulphur it contain 5 per cent. It yields in hydrolysis large amounts leucine and tyrosine and other substances similar to tho thus obtainable from proteids.

The various albumins we have spoken of belong to th animal body, but in the vegetable kingdom proteids ar found which do not differ in any essential particular fro animal proteids. The amount of proteid matter in plant is less than that found in animals, and globulins exist i

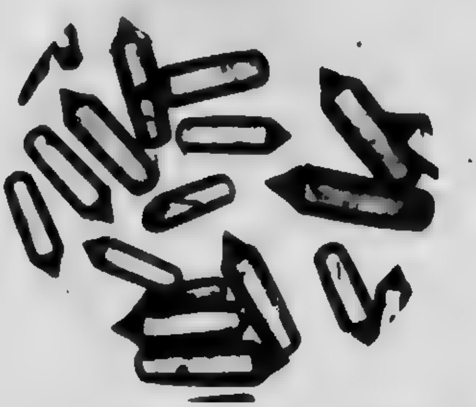

FIG. 159.—ALBUMIN CRYSTALS FROM HORSE-SERUM (GÜRBER).

larger amounts than albumins, in fact there are foo substances used by animals, oats, maize, peas, etc., i which it is said that the whole of the proteid occurs a globulin and none as albumin.

Some of the plant proteid matter crystallizes readil vitellin for example. It is this substance which ha furnished the so-called 'crystallized albumin,' the existenc of which has been known for some time. Egg-albumi may be readily crystallized and the serum-albumin horse's blood is remarkable for the ease with which it ma be obtained in a crystalline form (Fig. 159).

Both albuminates and proteoses occur in plants, bu peptone does not appear to be found in them.

The process by which plants form proteids is that of synthesis; it is possible that such substances as asparagine, leucine, tyrosine, etc., which are met with in the plant are on their way to tissue construction, and are not, as in animals, the result of proteid destruction.

A very remarkable fact about proteid substances is that, though they constitute the mainspring of organic life, yet they number amongst them, or amongst their decomposition products, some of the most powerful poisons known. Snake poison is a proteid, and even the albumose formed during the peptic digestion of albumin is highly poisonous if injected into the circulation.

The principal tests employed to detect the presence of proteids are as follows :

Proteid Reactions.

1. *Xanthoproteic Reaction.*—Solutions heated with strong nitric acid turn yellow, and on the addition of ammonia or caustic soda are changed to orange.

2. *Millon's Reaction.*—With Millon's reagent* they give a precipitate which turns red on heating.

3. *Piotrowski's Reaction.*—To the solution of proteid is added in excess a strong solution of caustic soda, and one or two drops of a weak (1 per cent.) solution of sulphate of copper; this gives a violet colour which deepens in tint on boiling. This test is also used to determine the presence of albumoses and peptones; the colour reaction given by these is rose-red on the first *careful and limited* addition of the sulphate of copper, turning to violet at once on the addition of any excess of the copper salt, and is termed the *biuret reaction.*

4. *Adamkiewicz's Reaction.*—To a solution of the proteid is added strong sulphuric acid and glacial acetic acid; a violet colour and slight fluorescence occur.

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* A mixture of mercurous and mercuric nitrates in presence of nitric acid.

5. Acetic acid and a solution of ferrocyanide of potassiu give a precipitate, except in the case of true peptones a some forms of albumose.

6. Acetic acid and sulphate of soda give a precipitate boiling, except in the case of peptones.

7. Saturation of the solution with neutral ammoni sulphate precipitates proteids other than peptones.

8. To a neutral or faintly acid solution of proteid ab lute alcohol is added in large excess, and a precipit obtained.

9. Heating a solution of proteid (albumins and globuli causes a coagulum to form. The solution should be r dered faintly acid with acetic acid, any excess of acid be avoided, as otherwise no precipitate may be produced.

The first three alone of the above reactions suffice detect the smallest traces of *any* proteid in solution.

There are many other tests for proteids, mercuric chlor lead acetate, etc., but the above are those which are pri pally employed either to determine their presence, or free a solution entirely from proteid.

Ferments.—The term 'fermentation' was originally plied to the characteristic phenomena which occur du the action of yeast in solutions of sugar, whereby the la is actively and rapidly converted into alcohol, and agent which gave rise to the phenomena was hence ca the ferment. Pasteur showed that in the case of alcoholic fermentation of sugar the active agent is yeast-cell, the process being dependent (as also in pu factions) on the activity of the cell as an *organized* li structure. Previously to this soluble substances, suc diastase from malt and pepsin from gastric juice, had obtained, and since the conditions under which they wo best, and many of the phenomena attending their a were closely similar to those holding good in the ca yeast, they also came to be called ferments. As more more of these 'substances' were discovered and supreme importance ascertained, as the causative age the chemical changes of digestion and numberless physiological processes, and, since they were all soluble in water and therefore devoid of any organized structure, they were called the unorganized ferments or *enzymes*. This division of the ferments into two classes held good, and is even now convenient, until a few years ago, when Buchner showed that a soluble, unorganized substance (zymase) can be extracted from yeast-cells, and is able to produce alcohol by its action on sugar. He obtained similar results with other (bacterial) organisms, so that we cannot now speak of any essential differences in the activities of the living (organized) ferments and the non-living (unorganized) ferments or enzymes.

Ferments are remarkable substances whose mode of action is still a mystery. The outcome of their action is usually hydrolytic—that is to say, they lead to the assumption of water by the substance on which they are working, and its decomposition into simpler, more stable bodies of smaller potential energy. We cannot, however, enter here into the details of ferment action, but must be content to point out the chief characteristics of their activity and properties. 1. They are inactive at sufficiently low temperatures, and work best at some given medium temperature, such as 40° to 45° C. Above this temperature the animal enzymes show a gradually diminishing activity, which is finally and irretrievably destroyed at 70 °C., or at once when their solutions are boiled. 2. Their activity is closely dependent on the reaction of the solution in which they work, whether it be acid, alkaline or neutral, as in the case of pepsin, trypsin, and ptyalin. 3. Their action is temporarily lessened or even stopped by the presence of an excess of the products of their activity, to begin again when these products are removed. This is well seen in a diastatic conversion of starch into sugar. 4. In some cases their action appears to be reversible; as, for instance, the inverting enzyme (maltase) of the intestinal juice can, if allowed to act on concentrated solutions of dextrose, reconvert a part of this into maltose. 5. They are all soluble in water, and conveniently so in glycerin. From these

solutions they may be precipitated by a sufficien
absolute alcohol or by saturation with neutral ammo
sulphate. When purified they resemble proteids in
position and reactions. 6. They are all non-diff
through membranes. 7. They are not apparently us
in the changes they produce, and they therefore inf
the velocity of any given conversion, not its total an
Thus, a trace of enzyme will *in time* effect the conv
of an unlimited amount of the substance on which
working: more of the enzyme merely hastens the r
which the final result is reached.

The enzymes in tissues do not always exist in a fr
active state, but as an inactive antecedent to whi
term *Zymogen* has been applied; a zymogen by
priate means may be converted into an active e
(see p. 234).

Of the **Pigments** of the body comparatively little is k
though they are widely distributed and perform imp
functions. The best known animal pigment is hæmo
the red colouring matter of the blood; it is of a
nature, yet crystallizable, and it also contains ir
acts as an oxygen carrier, and is often spoken of a
spiratory pigment; it has several derivatives (see pp
which supply the colouring matter of the bile, uri
partly that of the fæces.

The next pigment widely distributed is the black p
of the body or melanin; it occurs in the skin, hair (
eye, horn, and is the chief constituent of the m
tumours so common in the horse.

Both in the fæces and in the dandruff from the
the horse chlorophyll is found (p. 283); its functio
body is quite unknown.

The *bile pigments* have been sufficiently dealt
p. 220.

There are several other pigments, but none so in
as the above.

Nitrogenous Fats.—Though true fatty substances
no nitrogen, yet there are certain complex nitroge

and their derivatives which are found distributed in the body; the most important of these is

Lecithin, which is found in the white blood-corpuscles, the white matter of the brain, nerves, and spinal cord, semen, etc., and also in yolk of egg, where it is united with vitellin. Decomposition products of lecithin are *glycero-phosphoric-acid* and *choline*. The latter substance is poisonous, and by oxidation with nitric acid yields the extremely poisonous substance muscarine. Lecithin is largely introduced into the body by means of the food; the poisonous action of the choline it contains is probably prevented by the substance being broken up by the bacteria of the intestines into carbonic acid, marsh gas, and ammonia.

Neurine is a substance closely related to choline, but much more poisonous; it is the active principle in the poisonous alkaloids produced by putrefactive decomposition of animal matter.

Amides and Amido-Acids. — Many of the substances belonging to this series are of considerable importance, and very interesting from the point of view of their probable relationship to the formation of urea in the animal body.

Glycine, $C_2H_5NO_2$ (also known as glycocoll and glycocine), is amido-acetic acid, $CH_2(NH_2)COOH$. It does not exist in the free state in the body, but in union with benzoic acid, to form hippuric acid (p. 298), and with cholalic acid to form the glycocholic acid of bile (p. 222). It is very soluble in water, the solutions having an acid reaction but sweet taste, and it crystallizes readily.

Sarcosine, $C_3H_7NO_2$, is methyl-glycine, $CH_2NH(CH_3)COOH$. Chemically it closely resembles glycine, and though not found in the body is an interesting substance, owing to its chemical relationship to creatine and its discussional relationship to the question of how urea is formed in the body (p. 295).

Taurine, $C_2H_7NSO_3$, or amido-isethionic acid, is one of the constituents of the bile acid of carnivora, viz., taurocholic acid. It is a substance with a neutral reaction and is very stable, even when exposed to a high temperatu and boiling dilute acid and alkalis. In the intestin canal taurine in some animals, as man, is absorbed an reappears in the urine; in dogs a large part is excrete unaltered; in herbivora part is excreted and part oxidize leading to an increase of sulphates in the urine. It found in small amounts in horseflesh.

Creatine, $C_4H_9N_3O_2$.—This is the chief and characterist 'extractive' of muscle-substance, in which it is present the extent of 0·2 to 0·3 per cent. It is hence present large amount in 'meat-extracts,' from which it may ther fore most conveniently be prepared, and is easily obtai able, since it crystallizes readily. When boiled wi baryta-water it takes up a molecule of water and spl into sarcosine and urea (p. 295). When heated wi mineral acids it loses a molecule of water, and is there converted into

Creatinine, $C_4H_7N_3O$.—It is present in urine as a co stant and characteristic constituent, varying greatly amount, according to the amount of proteid in the food.

Lysatine (or *lysatinine*), $C_6H_{13}N_3O_2$, or $C_6H_{11}N_3O$, is homologue of either creatine or creatinine. It is an intere ing substance because it is obtained among the produ of decomposition of proteids by means of boiling hyd chloric acid and zinc chloride, and readily yields u when it is itself heated with baryta-water. In this the long-sought-for production of urea from proteids *purely chemical means* became for the first time an acc plished fact.

Leucine, $C_6H_{13}NO_2$, or amido-caproic acid, is a cha teristic product of the pancreatic digestion of proteids, is physiologically interesting, as a probable step, by changes it undergoes in the liver, in the formation of in the body (pp. 231, 293). It may also be obtaine large quantities by boiling horn shavings with sulph acid. It crystallizes readily, and in forms so easily cognizable and so characteristic that they afford an fallible means of determining the presence of leucin the minutest quantities (Fig. 160).

Aspartic Acid, $C_4H_7NO_4$, or amido-succinic acid, may be obtained by the decomposition of proteids during pancreatic digestion, or their hydrolysis with acids. It is also found in plants, but forms no part of the animal body. Closely related to this acid is *Asparagine*, $C_4H_8N_2O_3$, which is principally of interest in the proteid metabolism of plants, though it does not occur in animals. When taken into the body of the carnivora, asparagine is wholly converted into urea; with herbivora it would appear that a part of the nitrogen of the asparagine can take the place of proteid and be stored up. Considering the frequency with which asparagine exists in plants, the conversion of asparagine into proteid is a valuable provision.

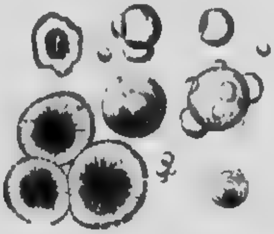


FIG. 160.—LEUCINE CRYSTALS (KRUKENBERG).

The Urea and the Uric Acid Group.—*Urea*, or *carbamide*, is the end product of proteid decomposition, and the chief nitrogenous constituent of the urine. It has the formula $(NH_2)_2CO$, and is found in minute quantities in some of the tissues of the body, though it is never found in muscle. In a pure state it crystallizes in long needles, but in the form of nitrate it separates out as six-sided tables arranged in piles (Fig. 68, p. 294), and as oxalate in crystals resembling the nitrate, but of prismatic form. Urea is very soluble in water, soluble in alcohol, but insoluble in ether. The crystals have a bitter taste somewhat resembling saltpetre. It may be easily obtained in quantity by concentrating urine to a syrupy state and extracting this with alcohol. The alcoholic extract then yields urea by slow crystallization.

Two modes of the artificial preparation of urea outside the body are peculiarly interesting. When *dry* ammonia and carbon dioxide are brought together they form carbamic acid, which at once unites with ammonia to form ammonium carbamate, $2NH_3+CO_2=NH_4NH_2CO_2$. Simple dehydration converts this at once into urea; hence the name carbamide, as being an amide of carbonic acid. Ammonium carbamate readily takes up one molecule of water to become ammonium carbonate. Urea may similarly be converted into ammonium carbonate by the assumption of two molecules of water, a change quickly completed by heating it in sealed tubes. The above purely chemical facts are important to the question of how urea is formed in the body (see p. 293).

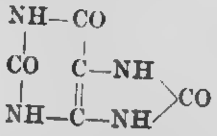
The second interesting synthesis of urea is by the action of ammonium sulphate on potassium cyanate; this yields ammonium cyanate, $NH_4.CNO$, which by mere evaporation to dryness is molecularly rearranged into urea, $NH_2.CO.NH_2$. The interest which attaches to this is that it was the first instance (in 1828) of the preparation by purely artificial means of a substance till then known only as a product of the living animal body.

When urine is allowed to stand it rapidly becomes highly alkaline, due to the conversion of the urea it contains into ammonia and carbonic acid under the influence of organisms such as the *Micrococcus ureæ*.

When urea is heated in a *dry* state for some time to 150° C. it gives off ammonia, and is largely converted into *biuret*. This substance yields a bright pink colour by the addition of sulphate of copper and caustic soda to its solutions. Since peptones (and some albumoses) yield a simila pink colour with the same reagents, it has come to b spoken of as the 'biuret reaction.'

Uric Acid has the formula $C_5H_4N_4O_3$. It is the chie nitrogenous constituent of the urine of birds and reptiles but only occurs in small quantities in the urine of the dog and is absent from that of the herbivora. It is a crystalline substance (Fig. 68, p. 297), odourless, tasteless, an extremely insoluble in water, very slightly soluble in ethe and alcohol, but readily soluble in caustic potash. Uric acid does not occur free in the urine, but as urates combined with bases. Apart from its characteristic crystalline appearance, uric acid is readily recognizable by evaporating a fragment of the suspected substance carefully to dryness on a piece of white porcelain with a few drops of *strong* nitric acid. If the substance is uric acid, the residue thus obtained may be yellow, but is frequently pink, and is certain to turn to a bright reddish purple under the influence of the fumes of ammonia. This is the well-known murexid test for uric acid, the colour being due to ammonium purpurate.

There is a very close chemical relationship between urea and uric acid, but there is nothing to account for the fact that snakes and birds turn out the nitrogenous end-products of their metabolism as uric acid, while mammals get rid of it as urea. The chemical relationship of uric acid to urea is at once apparent on mere inspection of the constitutional formula of the acid—



$$\begin{array}{llll} \mathrm{NH}-\mathrm{CO} & & & \\ \;| \qquad\; | & & & \\ \mathrm{CO} \quad \mathrm{C}-\mathrm{NH} & & & \\ \;| \qquad\; \| & & \rangle \mathrm{CO} & \\ \mathrm{NH}-\mathrm{C}-\mathrm{NH} & & & \end{array}$$

the groups on the right and left of the formula containing the obvious potentiality of becoming urea. In accordance with this we find that in nearly every possible decomposition of uric acid, whatever other substances are obtained, urea is constantly present among them.

We have previously dealt with the probable mode of origin of uric acid in the body, on p. 296, and have there also indicated its relations to the xanthine bodies as allied members of the purin group.

Allantoin, $C_4H_6N_4O_3$, is a substance found in the allantoic fluid, especially that of the calf, and in fœtal urine and amniotic fluid. It can be obtained from urine after the administration of uric acid, and from uric acid by oxidation with potassium permanganate.

The Aromatic Series.—Many members of this series occu
in the urine and some in the digestive canal.

Benzoic Acid, $C_7H_6O_2$, is found principally in the uri
of herbivora, and more commonly in stale than in the fre
secretion. In stale urine it is derived from the deco
position of hippuric acid. This acid does not exist free
the urine, but is combined with alkalis. It may be o
tained as fine glistening needles which give microscopical
the appearance presented in Fig. 71, p. 300.

This acid is not very soluble in water, but readily d
solves in alcohol and ether; on heating it sublimes,
which respect it differs considerably from hippuric ac
The source of benzoic acid in the body is discussed
p. 298.

Hippuric Acid, $C_9H_9NO_3$.—This acid exists largely
the urine of the herbivora; it is formed within the body
the union of benzoic acid with glycine, and may readily
found in fresh urine, though when decomposition occur
breaks up into its constituents.

Hippuric acid is found in the urine united to an alk
but may be obtained as a crystalline substance (Figs.
70, p. 299). The acid is not very soluble in water, bu
readily dissolved by alcohol; it is insoluble in petrole
ether, a fluid in which benzoic acid is soluble. W
heated *dry* in a small tube it yields a characteristic od
of new hay. The source of this acid in the body is
cussed on p. 298.

Tyrosine, $C_9H_{11}NO_3$.—This is found in many plants,
also in the intestinal canal as the result of the pancre
digestion of proteids. It is, in fact, the close compa
of leucine in nearly all the decompositions of prot
and other substances. In some ways it is less interes
physiologically than is leucine, since there is no evid
that it is in any way a forerunner of urea in the body,
so often said to be the case. On the other hand, it
great interest as indicating the presence or absenc
aromatic groups in substances which do or do not
tyrosine by hydrolysis. Thus gelatin yields no tyrosi

pancreatic digestion; it lacks therefore the aromatic group in its molecule, and consequently, unlike its allies the true proteids, gives no reaction with Millon's reagent (see p. 641).

Tyrosine crystallizes in fine needles which are sparingly soluble in water, insoluble in alcohol, but soluble in acids and alkalis. Tyrosine yields a very brilliant reddish pink colour when heated with Millon's reagent, if present even in minute traces, so that its identification is easy.

Phenol and *Cresol* are formed in the animal body during the putrefactive decomposition of proteids, and are excreted by the bowels and urine, in the latter being found as an ethereal salt of sulphuric acid. This phenyl-sulphuric acid is also formed from the aromatic compounds in the food, especially that taken by the herbivora (p. 301).

Pyrocatechin is found largely in the urine of the horse and other herbivora, and also after the administration of benzene or phenol. The dark colour of urine on standing, such as is well seen in the horse, is due to the oxidation of pyrocatechin. The source of this substance is from the phenol of the intestinal canal, and it may probably be introduced with certain constituents of the food (p. 301).

Indigo Series.—This contains several substances found in the urine and digestive canal.

Indol is the substance which gives the odour to fæces. It is present during the decomposition of proteids, and may be readily obtained from an artificial *putrefactive* pancreatic digestion, the odour of which is due to this substance.

Part of the indol leaves the body by the urine as a potassium salt of indoxyl-sulphuric acid, and if this be oxidized it may be made to yield indigo blue; if indigo blue be acted upon by powerful reducing agents it yields indol.

Indol administered to animals increases the output of indican, and whatever increases intestinal putrefaction increases the output of this substance; this is the reason why it is found more largely in herbivora than in carnivora (p. 300).

The presence of indican in the urine of the horse can readily be demonstrated by mixing the urine with an equal volume of hydrochloric acid, and adding a solution of hypochlorite of calcium until a blue colour appears.

Skatol is a substance closely allied to indol; it has much the same odour, and if excreted with the urine it passes off as a potassium salt of skatoxyl-sulphuric acid.

The Bile Acids.—These have been sufficiently dealt with on p. 222.

THE NON-NITROGENOUS BODIES.

Fats and Fatty Acids.—The fats met with in the animal body are compounds formed by substituting the radicles of certain acids of the acetic and acrylic series for the hydroxyls—OH—in the triatomic alcohol glycerin. The acids in question are the sixteenth and eighteenth in the acetic series — namely, palmitic and stearic — and the eighteenth of the acrylic series—oleic acid. The fats thus formed are therefore known as palmitin, stearin, and olein, and the mode of their formation is at once made clear by the following typical equation:

Palmitic Acid. *Glycerin.* *Palmitin.*

$$3(C_{15}H_{31}.COOH) + C_3H_5(OH)_3 = C_3H_5(C_{15}H_{31}.CO.O)_3 + 3H_2O.$$

A certain proportion of the fats in milk, and hence in butter, are formed, as above, from acids lower down in the acetic series, such as caproic, caprylic, and capric acid.

Fat is insoluble in water and only slightly so in alcohol, but freely soluble in ether, chloroform, and benzene. When pure it is neutral in reaction, tasteless and colourless, and by the action of caustic alkalis or superheated steam may be decomposed into its respective fatty acid and glycerin, the process being simply a reversal of the equation given above for the formation of a fat. When this splitting is brought about by an alkali the base, sodium or potassium, at once unites with the free fatty acid, and forms a salt which is what is known as soap. This decomposition and saponification take place to a greater or less extent in the intestine under the influence of the pancreatic juice and bile.

The solid fat of the body is composed principally of stearin, such as is found in the ox and sheep; the more liquid fat, such as is found in the horse and carnivora, contains more palmitin, but in all cases a mixture of the three fats is obtained. Fat as it exists in the cells of the living body is, of course, in a liquid condition. Since the melting-point of palmitin is 45° C. and that of stearin 55° to 60° C., it is evident that the fluidity of living fat is due to the olein it contains, whose melting-point is $-5°$ C.

The amount of fat in the body must depend upon the feeding of the animal, and will obviously vary within extreme limits. In individual tissues marrow has the largest amount; nerve, brain, milk, muscle, liver, bone, bile, and blood, have proportions which decrease in the order given.

The change which the fats undergo in the alimentary canal is discussed in the chapter on the Pancreas (p. 236), whilst the origin of fat in the body and its function is dealt with under Nutrition (p. 324).

Butyric Acid is found in the intestines, and in milk, it exists in union with glycerin as a neutral fat, and on the decomposition of this fat gives the odour to rancid butter. It may also be produced by the second stage of lactic fermentation in the stomach and alimentary canal, being derived from the carbohydrate matter ingested.

Glycerin, which since it is an alcohol should really be known as glycerol, is a viscid, colourless. sweet fluid, soluble in all proportions in water and alcohol, but insoluble in ether. When heated strongly it yields *acrolein,* a substance which gives the pungent odour to burned fat.

Lactic Acid exists in two forms in the body: ethylidene-lactic acid is the chief product of the lactic fermentation of sugars, and is found in the stomach and intestines especially after a diet containing carbohydrate; sarco-lactic acid occurs in muscles, and is the cause of their acidity after activity.

Cholesterin is a peculiar substance extracted originally from gall-stones. It can be obtained in sparkling crystals which are soapy to the touch, and of characteristic microscopical shape. Cholesterin is the only alcohol which occurs free in the body; it is not a fat, though, as a matter of convenience, it is generally dealt with in speaking of fats. Being an alcohol it should be called cholesterol. It is quite insoluble in water and *cold* alcohol, but readily soluble in solutions of bile salts, in ether and in chloroform. If an equal volume of strong sulphuric acid is added to a solution of cholesterin in chloroform the latter becomes at first blood-red, and then passes through blue and green to become finally yellow. This play of colours is very similar to that observed on the addition of nitrous acid to bile pigments (p. 220). If solid cholesterin be treated with strong sulphuric acid it turns red or violet, the colour changing additionally to blue or green on the addition of dilute solution of iodine. Cholesterin is thus a substance easily recognizable when present in even minute amounts.

Cholesterin is found in the nervous system, and is especially common in the pia mater of the cerebellum and plexus choroidea of the horse, where it may give rise to tumours, the nature of the growth being readily recognized from its silvery fish-scale-like appearance. It is also found in lanoline or wool fat and in dandruff, where it replaces the glycerin in the fat.

Carbohydrates.—This important class is of the greatest interest to the physiologist, inasmuch as the bulk of material consumed as food, especially in the herbivora, consists of carbohydrate matter. It is an extensive group of bodies consisting of such substances as starch and its derivatives, the various forms of sugar, and cellulose. Though so much carbohydrate material enters the body, but little can be found in the tissues. An animal starch (glycogen) may be found in the liver and other organs, minute amounts of sugar may be found in the blood, and a sugar exists in milk; but very much less carbohydrate is recoverable from the body than enters it as food, for the reason that the bulk of it becomes converted into fat (p. 325) or is rapidly oxidized to carbonic acid and water as a source of heat and energy to the body (p. 323).

The carbohydrates may be divided into the starch group or polysaccharides, the cane-sugar group or disaccharides, and the dextrose group or monosaccharides.

Polysaccharides, $(C_6H_{10}O_5)n$.

Starch.—The formula for starch is unknown; it is considered to be $(C_6H_{10}O_5)n$, where n is not less than 5 or 6, and is probably very much larger.

Starch exists in plants in the form of grains, the shape of which depends upon the group from which it is derived; thus potato, bean, wheat, and other starch grains have each a distinctive shape. The grain is composed of two parts, an envelope known as cellulose, and an interior called granulose. The granulose is the true starch; the cellulose is not, however, identical with the ordinary cellulose of plants.

Starch is insoluble in cold water, but when boiled the grains burst, and a viscid, opaque, pasty mass results which is not, however, a true solution of starch. A solution of starch can be obtained from this mass by *careful and limited* digestion with an enzyme, such, for instance, as human saliva, or by the action of dilute acid; when this takes place the material becomes watery, perfectly transparent, and filters readily, while previously this was impossible. To this limpid fluid the term soluble starch has been given.

The characteristic test for starch is the blue colour produced on the addition of iodine. Starch has no reducing action on Fehling's solution.

Dextrin.—When starch paste is acted upon by dilute mineral acid, or the enzymes found in the saliva and pancreatic juice, soluble starch is first formed as above described; but if the process be allowed to continue, further changes rapidly occur, leading to the production of dextrin

and finally of sugar. There are probably several dextrin
though two are generally more particularly described, vi
erythro-dextrin and achroo-dextrin. These are disti
guished from starch and from each other by their colo
reactions with iodine, erythro-dextrin giving a reddi
colour, while achroo-dextrin gives no colour. Much t
same change which can thus be brought about by acti
upon starch out of the body, takes place in a more perfe
and complete form within the body.

The conversion of starch into dextrin and finally in
sugar under the influence of certain enzymes, perfor
a most important physiological function; neither star
nor dextrin is capable of being absorbed as such, where
the sugar which results from this conversion is read
assimilable.

Glycogen closely resembles starch; it is found in seve
of the tissues of the body, and its origin and use in t
economy have been previously discussed (see p. 225).
may be obtained as an amorphous white powder, read
soluble in water, and gives with iodine a port-wine colo
instead of blue. By the action of acids or enzymes it
readily converted into dextrin, and finally into sugar. T
sugar resulting from the action of acid is dextrose, wher
that produced by the enzyme is maltose; in the liver t
sugar produced is dextrose and not maltose, and the meth
by which this conversion is obtained has been previou
dealt with (p. 229).

Cellulose, though not found in the animal body, is
great interest to the physiologist from its intimate relat
to the feeding of the herbivora. The food substance
plants is locked up in a cellulose envelope, and until t
envelope is broken down the material within cannot
acted upon by the digestive juices. This breaking do
is accomplished by laceration during the process of ma
cation, but also by a subsequent digestion of the coveri
by which means it is removed and the food substa
exposed.

The digestion of cellulose is a question which has gi rise to great discussion, inasmuch as no animal is known to secrete a cellulose enzyme, although many, such as the herbivora, are known to digest cellulose. Bunge states that sheep are capable of digesting 30 to 40 per cent. of the cellulose of sawdust and paper when mixed with hay.

The two views most generally held at the present time with reference to the digestion of cellulose are that it is either due to putrefactive organisms or to a specific enzyme.

Cellulose may be digested outside the body under the influence of putrefactive organisms, with the evolution of marsh gas and carbonic acid. Every condition necessary for this change exists within the body in most efficient form; for example, in the rumen of the ox, and the large intestines of the horse; but it would appear to be more than probable that a cellulose-dissolving enzyme exists. Young cellulose is more easily digested than old; it is certain that the older parts of the plant are converted into lignin, and this to the majority of animals must be insoluble.

Cellulose when treated with strong sulphuric acid is converted into a dextrin-like product, and is finally converted into dextrose.

Disaccharides, $C_{12}H_{22}O_{11}$.

Saccharose, or cane-sugar, is not found as part of the animal body, but exists largely in plants, and forms a well-known supply of carbohydrate to the system. Cane-sugar does not give some of the characteristic sugar reactions, among others it has no reducing action upon salts of copper, but by boiling with dilute mineral acids it is converted into equal parts of dextrose and levulose, and the same change may be effected by enzymes in the stomach and small intestines. This conversion of cane-sugar is recognised by the changed action of the solution on polarized light, the rotation of the plane of polarization being now left-handed instead of right-handed as it was previously to the conversion, that is to say inverted; he the name invert sugar.

If cane-sugar be injected into the circulation it pas out unaltered; it is certain that before this sugar can assimilated it must be converted into dextrose.

Maltose is formed by the action of malt extract (diasta on starch paste, also by the action of saliva and pancrea juice upon starch paste or glycogen. In its reaction corresponds closely to dextrose, but it has a one-third reducing action upon Fehling's solution, and it does reduce Barfoed's reagent,* which dextrose is capable doing. Its specific activity in rotating the plane polarized light is considerably greater than that of d trose, being about +140° as against +52° for dextro If 5 c.c. of a ½ per cent. solution of maltose is warmed half an hour on a water-bath together with 1 decigram of phenyl-hydrazine hydrochloride and 2 decigrammes sodium acetate, a yellow compound is obtained in char teristically shaped crystals. These are phenyl-maltosazo $C_{24}H_{32}N_4O_9$. When heated the crystals melt at 206° and this, together with the shape of the crystals and th specific solubility in 75 parts of boiling water, renders identification of maltose easy.

Maltose is, like cane-sugar, non-assimilable, for injected into the circulation it is excreted unchang and it is probable that before absorption it has to converted into dextrose.

Lactose, or milk-sugar, is found solely in milk. reduces Fehling's solution, and has the same rotat power as dextrose, but it does not reduce Barfoed's reage nor does it undergo direct alcoholic fermentation w yeast. If boiled with dilute mineral acids it is conver into equal parts of dextrose and galactose.

Lactose readily undergoes lactic fermentation, as, instance, in souring milk. The cause of this is a mic organism; but there are reasons for believing that enzyme may also bring it about.

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* A solution of cupric acetate to which acetic acid is added.

In spite of the fact noted above, that isolated lactose is unable to ferment in the presence of yeast, yet an alcoholic fermentation is capable of occurring in milk, such, for instance, as in the koumiss from mare's milk, and kephir from cow's milk. It is probable that the changes which bring this about are very complex, and due to several organisms.

Lactose, like saccharose and maltose, is non-assimilable as such, and it is probable that it is changed into dextrose before absorption, not necessarily as the result of the action of any digestive secretion, but during its passage through the intestinal wall.

Like maltose, lactose yields an osazone, phenyl-lactosazone, which crystallizes in characteristic rounded clumps of yellow crystals. These crystals melt at 200° C., and are soluble in 80 to 90 parts of boiling water.

Monosaccharides, $C_6H_{12}O_6$.

When the members of the preceding group of sugars, the disaccharides, are boiled with dilute acids or otherwise hydrolyzed, they take up a molecule of water and split into two molecules of a new sugar. Thus cane-sugar yields dextrose and levulose, maltose gives two molecules of dextrose, and lactose yields dextrose and galactose. Of these the most important is:

Dextrose, Glucose, or *Grape Sugar*.—This is probably the form to which all sugars must be reduced in the alimentary canal, whether before or during absorption, in order that they may be assimilable by the tissues.

In its ordinary reactions dextrose resembles maltose, but may be easily distinguished from it by the following differences in behaviour.

Its specific rotatory power is only +52°. It reduces Barfoed's reagent (see Maltose). The osazone it forms, phenyl-glucosazone, crystallizes in fine yellow needles; these melt at 205° C. and, unlike the corresponding compound of maltose, are almost insoluble in water.

Dextrose is capable of undergoing three fermentation viz., alcoholic, lactic, and butyric; the two latter ar probably always present in the intestinal canals of animal especially after a carbohydrate diet.

Levulose.—This occurs in fruits and honey, mixed wit glucose; it may also be prepared by acting upon can sugar with sulphuric acid, by which means the cane-sug is converted into equal parts of dextrose and levulose.

Inosite, $C_6H_{12}O_6$. $(CH.OH)_6$.

This is a crystallizable substance, found among th 'extractives' of many tissues, usually in very minu quantities, though it is markedly present in heart-musc and in horse-flesh, which may contain as much as ·008 p cent. It occurs also in semen. Inosite is found abundant in vegetable tissues, especially in unripe beans, which th provide a convenient source for its preparation. Possess of a sweet taste, and as being originally found in muscl inosite has at times been called 'muscle-sugar.' B although its empirical formula is the same as that of monosaccharide, it is not a sugar at all: its solutions exe no rotatory power on polarized light, do not reduce metal salts, and form no osazone with phenyl-hydrazine, nor a they capable of undergoing alcoholic fermentation. It in fact a member of the benzene series, and consists of closed ring of six CH.OH groups.

The sugars of chief physiological importance are, as have seen, the hexoses, that is to say a sugar such dextrose which contains six atoms of carbon in the molecu or the disaccharides which contain twelve. But the rec progress of organic chemistry has led to the synthesis only of the sugars which are ordinarily met with, but o series of artificial sugars containing three (trioses), fo five (pentoses), seven, eight, and nine atoms of carbon their molecule. Of these the pentoses alone at pres possess any physiological interest. This is due to the f that a *pentose* may be obtained by the decomposition of the nucleo-proteids of the pancreas and of yeast-cells. These pentoses are not assimilable, as shown by their rapid appearance in the urine after their introduction into the body. Pentose yields an osazone which melts at 160° C.

Tests for Sugar.

1. *Trommer's.*—An excess of caustic potash and a small amount of dilute solution of copper sulphate is added to the fluid and the whole heated. The copper is reduced to suboxide by the sugar and a red precipitate falls. Fehling's solution, which is used as a *quantitative* test for sugar, consists of hydrated cupric oxide in caustic soda, and the double tartrate of sodium and potassium. This is made to contain such an amount of the cupric oxide in each cubic centimetre as is exactly reduced, and the blue colour destroyed, by 0·005 gramme of dextrose. The principle of this test is the same, viz., the reducing action of the sugar, which robs the cupric compound of its oxygen.

2. *Moore's.*—A solution of sugar boiled with caustic potash turns brown.

3. *Böttcher's.*—Bismuth oxide and excess of caustic potash are added to the fluid containing sugar and heated; the solution becomes grey and then black, from the deposition of metallic bismuth.

4. *Picric Acid Test.*—Boil the solution of sugar with a little picric acid and caustic soda in small quantities; a brown-red opaque coloration is obtained.

5. *Fermentation Test.*—The fluid containing a piece of yeast is placed in a tube and inverted over mercury; if sugar is present it undergoes fermentation, and carbonic acid is given off, which collects in the tube.

The osazone tests have already been described under the respective sugars. They are very important for the discrimination of the various sugars, as well as for their identification.

Inorganic Constituents.

The inorganic substances found in the body a water, gases, and salts. *Water* forms about 60 per cen of the whole body; it is taken in with the food ar drink, and a small quantity may be formed within t system.

The amount of water consumed by animals depends up the nature of their food and the class of animal. Hors fed on dry food consume more water than cattle, the fo of which contains as a rule a considerable amount water.

An excess of water leads to body waste by carrying the solids through the kidneys, whilst reduction in t amount of water produces thirst and loss of nutrition.

The *Gases* found in the body are oxygen, nitrog hydrogen, carbonic acid, sulphuretted hydrogen and mar gas. The two former are taken in with the inspired a carbonic acid is formed in the tissues, while hydrogen a its compounds are formed in the intestinal canal as t result of cellulose and other decompositions.

The largest portion of the inorganic matter consists the various *Salts* of sodium, potassium, calcium, magnesiu and iron, in the form of chlorides, sulphates, phosphat and carbonates. The distribution of these salts through the tissues is very variable; some, like bone, are excessiv rich, whilst others are remarkably poor in them. Cert tissues and fluids have a preponderance of some salts to exclusion of others.

The amount of the salts existing in the body depe upon the age of the animal, and their nature is modified the character of the food. The daily quantity ingested stored up is largely affected by the rate of growth, yo growing animals storing up material which the ac rejects.

The diet of the herbivora furnishes considerably m potassium than sodium salts to the system, with the re that in the excretions salts of potassium are in excess over those of sodium.

Sodium and *Potassium*.—Owing to the poorness of vegetable food in sodium salts, Bunge believes that the administration of common salt with the food of herbivora is a necessity. As this view is open to question his arguments in the matter should be known.

Bunge says that in spite of the many inorganic salts found in the food, one only, viz., sodium chloride, is taken separately by the human subject in addition to that already existing in the food. But carnivora avoid salted food, as sufficient sodium chloride exists in the blood and tissues in the raw state in which these are consumed by them. Herbivora, on the other hand, have been known to travel considerable distances to obtain salt.

According to Bunge the explanation of the desire shown by herbivora for common salt lies in the large amount of potassium consumed in their diet, the effect of potassium salts in the blood being to withdraw sodium salts from the system.

Here are some tables given by him to show the proportion potassium bears to sodium in various articles of diet.

In every 1,000 parts of dried material :

	Potassium.	*Sodium.*
Rice	1 ...	·08
Bullock's blood	2 ...	19
Oats Wheat Rye Barley }	5 to 6 ...	·1 to ·4
Dog's milk	5 to 6 ...	2 to 3
Peas	12 ...	·2
Milk of herbivora	9 to 17 ...	1 to 10
Hay	6 to 18 ...	·3 to 1·5
Beef	19 ...	3
Beans	21 ...	·1
Clover	23 ...	·1

For one equivalent of sodium the equivalents of potassi are:

	Equivalent K_2O.
Mangel-wurzel	2
Milk of herbivora	·8 to 6
Beef	4
Wheat	12 to 23
Barley	14 to 21
Oats	15 to 21
Rice	24
Rye	9 to 57
Hay	8 to 57
Peas	44 to 50
Clover	90
Beans	110

The preponderance of potassium over sodium salts is h most marked, and Bunge considers that when a relation from 4 to 6 equivalents of potassium to 1 equivalent sodium is obtained in a diet no addition of sodium chlor is necessary; but where the proportion of potassium higher than this the animal instinctively seeks for sodiu for the reason previously given.

We do not deny the stimulant to the palate wh common salt may afford the herbivora, but so far as hor are concerned, and we think the same argument m apply to cattle, it is quite certain that no addition common salt to the ordinary diet is necessary, and that food furnishes ample sodium for the purposes of the bod

Calcium forms the largest mineral deposit in the bod it is taken in by means of the food. Bunge states tha is probable that the lime salts required for the growth bone in young animals are contained in some orga compound, and that the administration of inorganic co pounds of lime in rickets is irrational and useless.

Lime exists largely in clover and hay, but only in sm quantities in the cereal grains; it is principally in the h that the amount excreted by horses through the kidney supplied. In the urine it passes from the body in s quantities that it cannot be held in solution by the alkal fluid, and the urine of the horse is therefore always turbid. In the body calcium exists in the form of phosphate, sulphate, and carbonate, in the urine principally as carbonate and oxalate.

Magnesium salts occur in the body principally as phosphates, and in this form they enter largely into certain foods, such as oats. The amount of magnesium passing away from horses through the kidneys is small, but considerable quantities derived from the food pass out with the fæces, as they cannot be utilized in the body. By collecting in the bowels this salt produces the ammonio-magnesium phosphate calculi so common in horses.

Phosphates are united with soda, potash, lime, and magnesia. They are principally taken in with the food, but may also be formed in the body from the metabolism of phosphorus-containing compounds. The foods richest in phosphoric acid are oilcake and bran, while hay and straw are poorest in this substance. Phosphoric acid is principally excreted by herbivora with the fæces, only small quantities passing away with the urine.

Carbonates are found in several of the secretions of the body, notably in the urine, where they cause the most intense evolution of gas on the addition of an acid. The carbonates in the system of the herbivora result from the carbonates of the food, and the combustion of organic acids, malic, citric, tartaric, etc.; these enter the body as salts of sodium and potassium, and the bases being set free unite with carbonic acid to form carbonates.

The *Sulphur* in the body is derived from the albumin of the food; in the system it is converted into sulphuric acid, and in this form 80 per cent. of the ingested sulphur appears in the urine. Sulphur exists in horn, hair, and epidermis.

The importance of the sulphates in the urine is considerable, as they afford a passage out of the body for the products of proteid decomposition. Phenol and allied compounds are in this way got rid of in the form of phenyl-sulphate of potassium.

Iron is an important constituent of the complicat substance hæmoglobin. It is also found in the hair, ski bile, lymph, most body fluids and tissues, and a sma quantity in the fæces. Bunge considers that the ir which enters the system can only be absorbed when in th form of an organic compound. Inorganic iron, thoug largely used in the treatment of certain diseases, is n absorbed from the intestinal canal; food contains on organic and not inorganic iron, and the hæmoglobin of th blood is formed from the complex organic compounds iron which are produced by the vital process of the plant.

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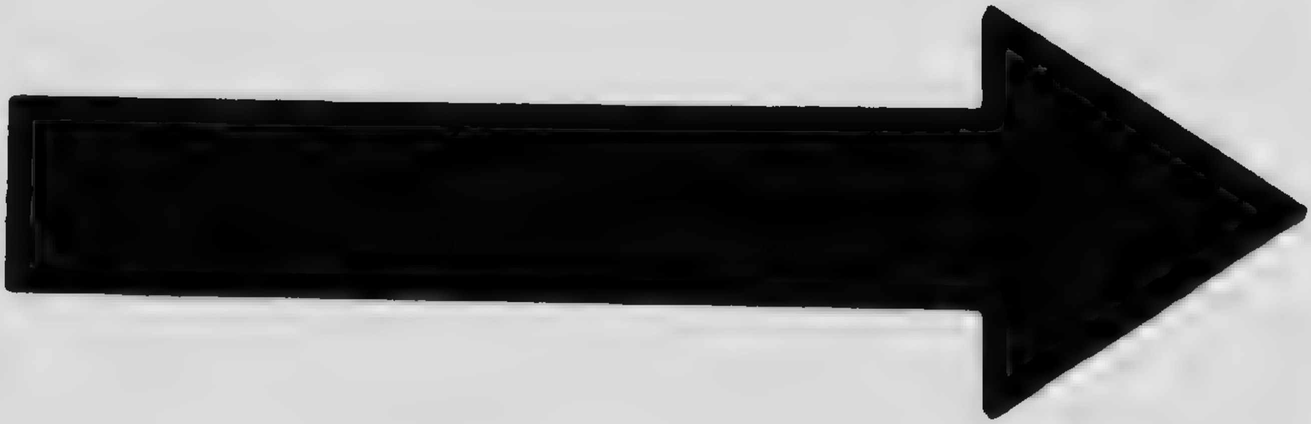

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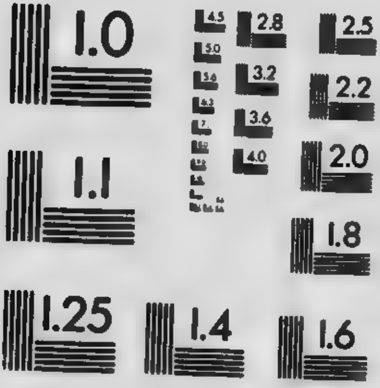

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